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## Cretaceous Nerineacean gastropods

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CRETACEOUS NERINEACEAN GASTROPODS: SYSTEMATICS,  
AFFINITIES AND PALAEOECOLOGY

PhD.

A thesis submitted for the Degree of Doctor of Philosophy

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December 1988

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**This thesis is dedicated to the memory of**

**ALISON HELENA WEST**

**a very dear friend**

## ABSTRACT

The Nerineacea form a distinctive and significant component of shallow marine Mesozoic Tethyan macrofaunas. They occur in shelf sediments deposited in tropical regions during the Jurassic and Cretaceous. The group first appears in the early Jurassic and high diversity levels had developed by late Jurassic and early Cretaceous times. A major extinction episode occurred during the latter part of the Cenomanian and the Turonian, with the Nerineacea becoming finally extinct in the Maastrichtian.

The heterostrophic nature of the nerineacean protoconch (described here from Nerineidae and Nerinellidae species) indicates opisthobranch affinities. The Nerineacea is placed in the Entomotacniata, an independent order within the Opisthobranchia. The Entomotaeniata is considered to show greatest affinities with some members of the Acteonacea. The Pyramidellacea are not included in the Entomotaeniata. The order contains the Ceritellidae, Nerineidae, Nerinellidae and Itieriidae. Early phylogenetic separation of the first three families is indicated. Within each family a limited number of "stable" internal fold patterns developed independently which reflected anatomical features of the abapical portion of the nerineid animal.

The Nerineacea typically inhabited warm, clear, carbonate-dominated shallow marine environments on and around off-shore "highs", however, some genera lived in prelittoral or lagoonal situations. Only *Ptygmatis* shows any evidence of tolerance of abnormal salinities. Carbon and oxygen isotope analyses demonstrate that *Nerinella* and *Simploptyxis* specimens from Austrian Gosau deposits lived in water of normal marine salinity. Most Cretaceous nerineid genera were probably mobile epifaunal herbivores, although Nerinellidae species may have been infaunal.



Cretaceous Nerineacea are taxonomically reviewed; the diagnoses of the subfamily Umboneinae; *Diozoptyxis*, *Adiozoptyxis*; *Julesia* and *Phaneroptyxis* are revised. Stratigraphic and palaeogeographic ranges indicate that certain species could potentially be used for correlation. Quantitative measurements of various parameters are included in specific descriptions; the value of these in specific resolution is tested in appropriate cases. An analysis of morphological range in one species (*Diozoptyxis cochleaeformis*) demonstrates wide continuous variation in overall shell shape and whorl concavity. However, external ornament and internal fold pattern do not show significant intraspecific variation; these features therefore provide reliable characters for species definition.

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# CHAPTER 1

## **INTRODUCTION AND PREVIOUS WORK**

### **1.1 DEFINING FEATURES OF THE NERINEACEA**

The Nerineacea are a large superfamily of extinct Mesozoic gastropods. Representatives of the group first occur in Lower Jurassic strata of Hettangian age (Cossmann, 1896); they disappear from the fossil record in the Upper Cretaceous (Maastrichtian, Dietrich, 1925; Sohl, 1987).

A variety of shell morphologies are included within this superfamily, all of which are united by the possession of three distinctive characteristics (figure 1.1) :-

- 1     a selenizone adjacent to the suture resulting from a juxtasutural slit or sinus at the adapical end of the aperture
- 2     opisthocline growth lines
- 3     a short siphonal canal terminating the aperture abapically.

These gastropods were restricted to the warm water of tropical and sub-tropical regions (Sohl, 1969) within which they inhabited a variety of shallow marine environments.

### **1.2 DESCRIPTIVE TERMINOLOGY**

The shells of the Nerineacea show a number of unusual features which do not commonly occur in other gastropod groups. The specific terminology for some of these features may be unfamiliar to non-specialists, as may some of the problems encountered in the description of nerineid shells. A brief discussion and illustration of the most common terminology employed and the difficulties encountered is therefore given here.

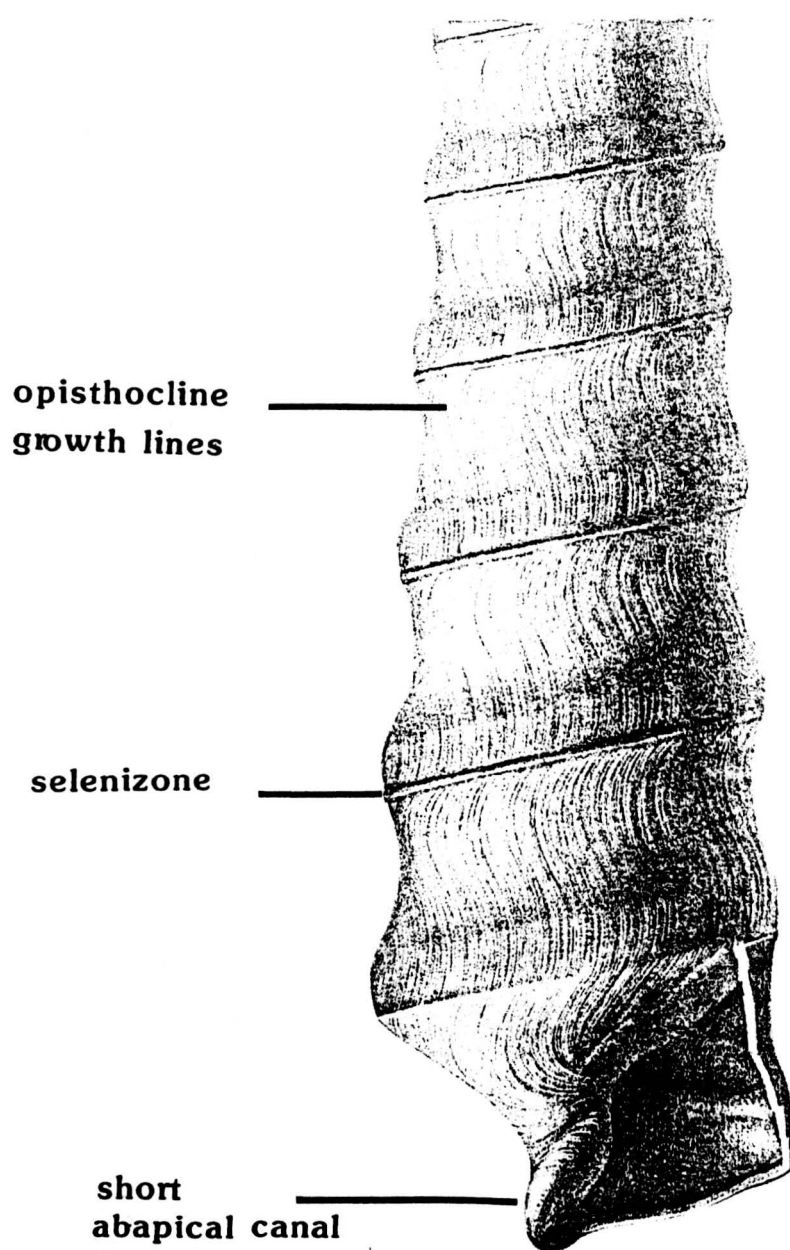


Figure 1.1 Defining characters of the Nerineacea. *Nerinea desvoidyi* d'Orbigny after d'Orbigny 1852, plate 261.

The nerineid aperture shows several important characters diagnostic of the group; the terminology used to describe the relative positions of these is given in figure 1.2. The most important is a slit or sinus in the apertural margin at the posterior (adapical) end of the aperture. This slit is therefore adjacent to the suture and incremental growth there generates a juxtasutural selenizone or slit band. The selenizone is found in all nerineids (if preservation is sufficiently good) and consists of a narrow band with chevron shaped growth lines pointing adapically. The growth lines of nerineid shells are consequently opisthocline: ie they curve adapically ("backwards") as shown in figure 1.1, reflecting the original backward curve of the aperture.

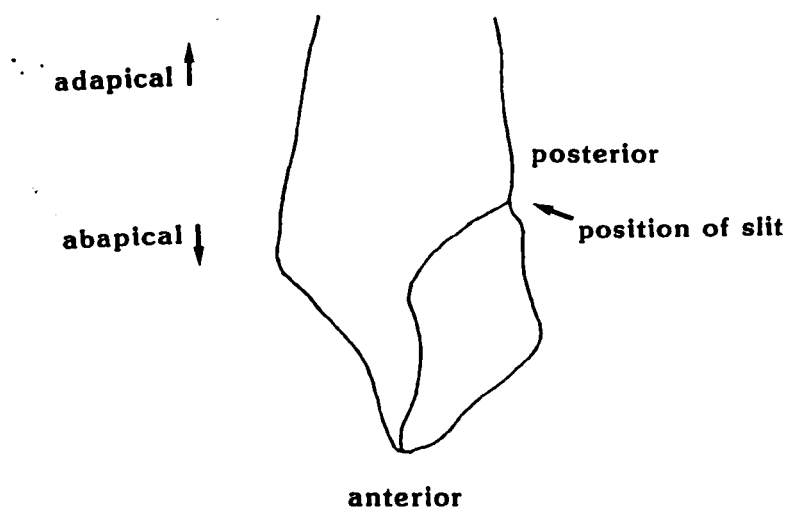
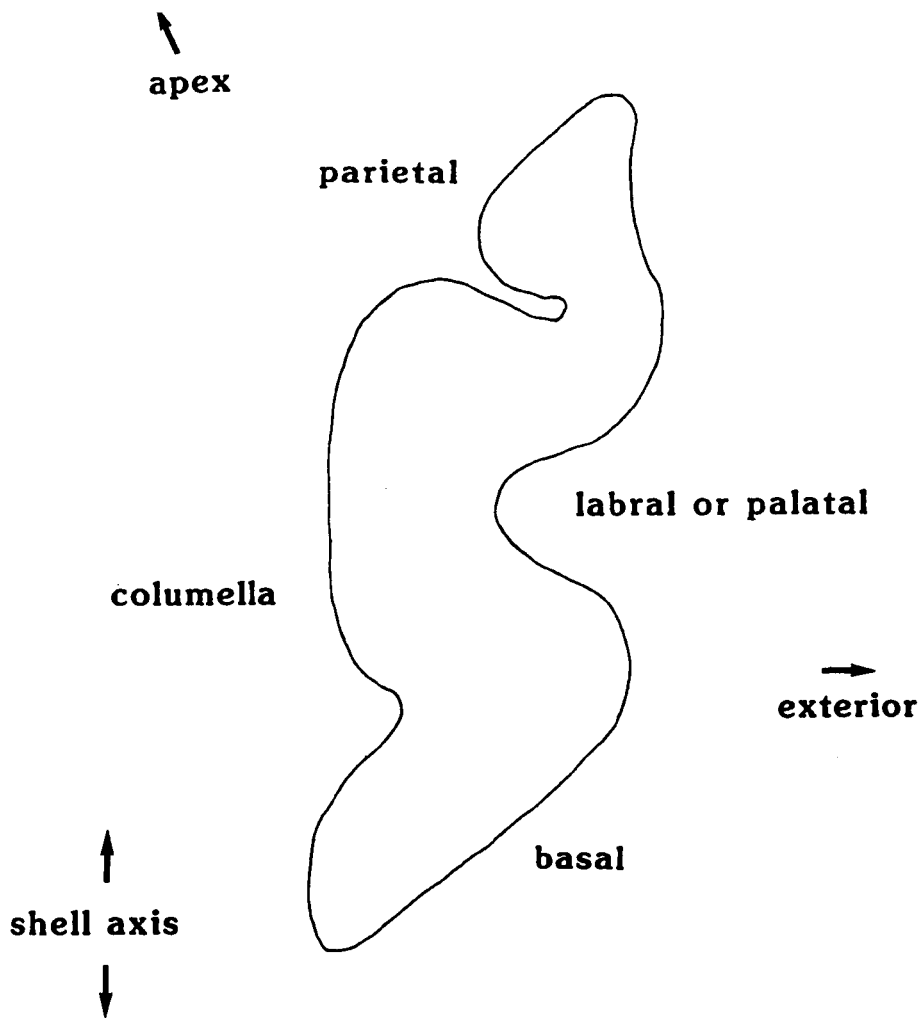


Figure 1.2 Spatial terminology used in gastropod shell and aperture description

Nerineids often have internal folds projecting into the whorl cavity. These folds tend to be very constant in nature, both within a single specimen (excepting the very earliest whorls and the region approaching the aperture), and also within species. The number, position and nature of the folds are therefore essential components of any species description.



**formula 1,1,1,0**

Figure 1.3 Median longitudinal section of one whorl showing three simple folds; one columella, one parietal and one labral. Fold formula is therefore 1,1,1,0.

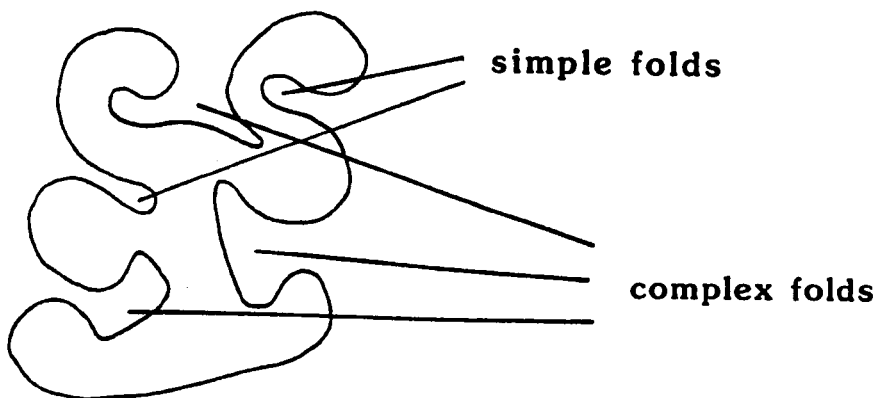


Figure 1.4 Median longitudinal section of one whorl showing a combination of simple and complex folds. Fold formula is 2,1,2,0.

Figure 1.3 gives the terminology used to specify the position of folds within the whorl, and the orientation of these with respect to the shell as a whole. Fold configuration can be represented by means of a simple formula which enumerates the number of folds on each whorl wall, starting with the columella, then parietal, labral and finally basal walls; this is also illustrated in figure 1.3. In many earlier works, parietal folds were treated as columella folds, with distinction being drawn only between folds on the "inner lip" (ie columella and parietal walls) and folds on the "outer lip" (ie labral and basal walls).

The folds may be either "simple", ie straightforward flexures projecting from the whorl wall, or they may be "complex", showing a tendency to bifurcate into lobes (see figure 1.4).

Gastropod shells are almost universally figured apex uppermost in English texts, however, some Continental workers, particularly the French, tend to figure shells with the aperture uppermost. This can lead to considerable confusion, particularly in earlier works where the positioning of folds or apertural features are described in terms of "upper" and "lower".

A common external feature of nerineid shells is that of a "bulging out" or swelling in the region of the suture. This swelling, known as a sutural ramp, can be symmetrical or asymmetrical about the suture and may show coarse knotted or tubercular ornament.

Some groups of nerineids have hollow columellas, where the shell has grown spirally around a space or umbilicus in the centre. There are often extensions of the abapical end of the whorl projecting into the umbilical space which are referred to as intraumbilical carinae (figure 1.5).



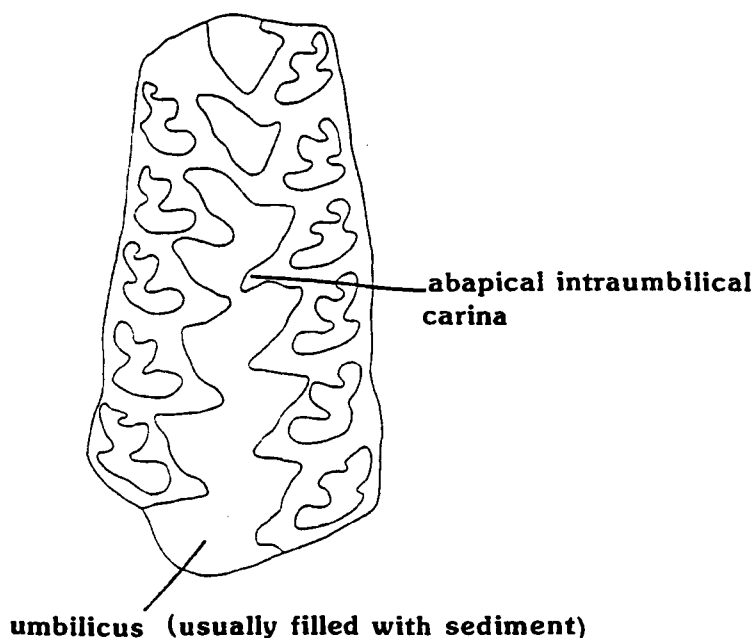


Figure 1.5 Median longitudinal section of an umbilicate species (*Pchelinsevia toucasiaephila* (Dietrich)) showing umbilical space and abapical carinae.

### 1.2.1 Note on Terminology Used

The following non-Latin terms are used throughout this thesis in the following sense:-

"nerineacean" and "nerineid" - both of these terms are used to cover the Superfamily Nerineacea.

"itieriid" - referring to members of the Family Itieriidae.

"ceritellid" - referring to members of the Family Ceritellidae.

"nerinellid" - referring to members of the Family Nerinellidae.

## 1.3 PREVIOUS WORK

### 1.3.1 Introduction

The remainder of this chapter consists of a review of previous study of the Nerineacea. It is not comprehensive; only the most important and significant work has been included. The section is arranged in strictly chronological order so that the evolution of ideas and the

sequence of critical revision can be clearly distinguished. Many of the systematic problems connected with the Nerineacea are complex and involved; the review has therefore not included appraisal of these problems, which are discussed, where appropriate, in subsequent chapters.

This review covers the taxonomic development of the group, from the establishment of the first genus and other significant genera to the creation of Families, Superfamily and Order. The various ideas concerning the affinities of the group with other gastropods are also reported, as are the different approaches to generic discrimination which have been used. The following trends can be distinguished:-

- 1 a rapid rise in the number of genera and species.
- 2 itieriid and ceritellid groups show a parallel conceptual development with Nerineidae genera; unification occurs much later.
- 3 gradual recognition of the posterior sinus, selenizone and anterior canal as unifying characters with increasingly less emphasis on the possession of folds.
- 4 repeated association of the group with cerithiids and pyramidellids, particularly in earlier works; more recently muchisoniids and acteonellids have also been proposed as relatives.
- 5 various approaches to generic resolution which have concentrated on one or a few characters have proved ultimately to be unsatisfactory except at a merely functional level.

### 1.3.2 Establishment of *Nerinea*

DeFrance (1824) proposed the name "*Nérine*"<sup>1</sup> for a genus which he proposed to receive some thick turriculate shells bearing folds on the columella and labral walls of the whorl

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<sup>1</sup>Original spellings, which were not always consistent, have been used, and original use of italics followed.

cavity. He described the shells as umbilicate with a thick columella and a canal terminating the aperture anteriorly. Defrance included within the new genus two species which he had distinguished but not named, together with some specimens collected by Deshayes at St. Mihiel and some from Neustadt figured by Knorr.

The "*Nérines*" were considered to be close to the "*Cérites*" although differences in internal structure between the two were noted (Defrance, 1824). In a later paper (Defrance, 1825) a possible affinity with the "pyramidelles" was mentioned and a "*nériné*" species figured ("*Nériné tuberculeuse*" Defrance).

The term "Nériné" or "Nérinée" was latinized by both Deshayes (1827) and Blainville (1827) by the introduction of the term "*Nerinea*". Blainville (1827) mentioned the group as a subgenus within the genus "*Cérite*" ("*Cerithium*") and gave a brief generic diagnosis based on that of Defrance (1824 and 1825); the species "*Nériné tuberculeuse* Defrance" was figured. Deshayes (1827) discussed the possible relationships of the group, concluding that the "Nérinées" were close to the "Cérithes" while acknowledging certain similarities to the "Pyramidelles". A generic diagnosis similar to that of Defrance (1824 and 1825) was formally proposed (Deshayes, 1827) and the species "*Nerina Mosae*"<sup>1</sup> described. This species was later figured (Deshayes, 1831). The validity of these various attempts to establish a genus and the implications for the original authorship and type species of *Nerinea* are discussed in Chapter 2.

The number of species in the genus greatly increased after the work of later authors (Zieten, 1830; Sowerby, 1836; Bronn, 1836; Roemer, 1836) and most palaeontologists of this period regarded *Nerinea* as a genus close to the "Cérites" (Rang, 1829, Holl, 1830) although Pusch (reported in Bronn, 1836) considered the group as ancestral to the pyramidellids, and Deshayes (reported in Bronn, 1836) thought the "Nérinées" were a connecting link between the pyramidellids and Lamarck's "Canalifera".

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<sup>1</sup>"*Nerina*" was presumed to be a misprint of *Nerinea* by Cox (1949).

The generic diagnosis proposed by DeFrance (1824) remained virtually unchanged until Voltz (1836) made a number of extremely perceptive observations concerning the characteristics of the genus. He noted the presence of a juxtasutural slit at the posterior end of the aperture, the slit band generated during growth and also the "backward pointing" (ie opisthocline) growth lines. The absence of folds at the aperture, and their progressive emplacement behind the aperture was noted both by Voltz (1836) and Roemer (1836); both also pointed out the common occurrence of concave whorls within the genus. Voltz formally stated that non-umbilicate species should be included within the genus (both DeFrance (1824 and 1825) and Deshayes (1827 and 1831) had specified a perforated columella within their diagnoses of the genus). Deslongchamps (1842) agreed with most of Voltz's observations although he was doubtful of the existence of a posterior juxtasutural sinus, having been unable to find either this or opisthocline growth lines on his own specimens. Interestingly, Deslongchamps (1842) reported two species appearing externally to be "Nérinées" but lacking internal folds, thus compelling him to place them in the "Cérîte" genus.

### 1.3.3 Development of Associated Genera

Matheron (1842) described a new genus, *Itieria*, consisting of subvoid to subcylindrical shells with later whorls enveloping earlier ones, a narrow aperture terminating anteriorly in a rudimentary canal and internal folds on the columella and labrum. He discussed the resemblances of this genus to both the "Nérinées" and the "Actéonelles", concluding that sufficient differences existed between *Itieria* and these two groups for the former to be treated as a distinct genus. Only one species of *Itieria* (which therefore became the type species of the genus by monotypy) was described and figured by Matheron (1842). In a footnote to the article, d'Orbigny claimed precedence for the authorship of this species as *Tornatella Cabanetii* d'Orbigny (1841) and disputed the validity of the new genus, considering it to be synonymous with "*Tornatella*" or "Actéon". D'Orbigny (1852) later included this species in *Nerinea*.

D'Orbigny (1843) substantially added to the number of *Nerinea* species; he considered the group to be close to the "Pyramidelles".

Morris and Lycett (1850) proposed a new genus, *Ceritella*, to include turreted shells with sulcated whorl margins, a short apertural canal, a smooth columella and overlapping last whorls. This new genus was distinguished from *Cerithium* by a more elongate aperture and large enveloping last whorl, and from *Terebra* by its smooth columella. The position of *Ceritella* was uncertain, although it was placed adjacent to *Nerinea* in the text. Piette (1857) erected two genera, *Fibula* and *Tubifera* both of which were similar to *Ceritella*. *Fibula* was characterised by a posterior notch adjacent to the suture, a short apertural canal, an umbilicus and a straight columella; Piette suggested this genus resembled "*Cerithium*" and some "Turritelles". *Tubifera* showed a cylindrical shape, with elongate straight whorls, the last one overlapping, and a canal terminating the aperture abapically.

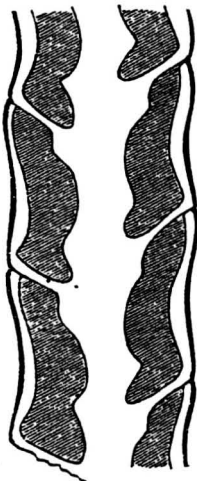
#### 1.3.4 Subdivision of *Nerinea*

By 1850, about 100 *Nerinea* species had been described (Zieten, 1830; Bronn, 1836; Sowerby, 1836; Roemer, 1836; Philippi, 1837; d'Orbigny, 1843; Goldfuss, 1844; Zeuschner, 1850). Sharpe (1850), accepting the systematic unity of most of the described species of *Nerinea*, made the first attempt to divide the genus. Four subgenera were erected, primarily on the basis of fold structure and overall morphology; *Nerinea*, *Nerinella*, *Prygmatis* and *Trochalia* (see figure 1.6). Existing species were divided between these subgenera and further informally subdivided into umbilicate and non-umbilicate forms where appropriate, although Sharpe did not consider the presence or absence of an umbilicus to be a reliable character for taxonomic purposes. He cited the case of *Nerinea voltzii* Deslongchamps which was described as imperforate in early ontogeny, becoming umbilicate in later life. The possession of internal folds was, for Sharpe, an essential generic character; he also suggested that the "filling up" of the whorl cavity by the folds at the shell apex was related to abandonment by the animal of this

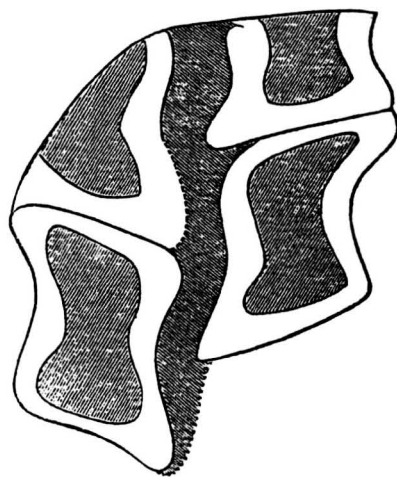
section of the shell which could then be eroded off. Sharpe saw *Nerinea* as intermediate between "*Trochi*" and "*Cerithia*"<sup>1</sup>. *Nerinea* was considered to have been a littoral animal, most commonly occurring in carbonate facies (Sharpe, 1850).

Figure 1.5 The diagrams given by Sharpe (1850) to illustrate his subgenus diagnoses.

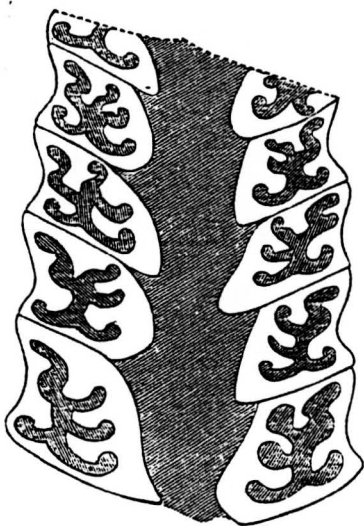
*Nerinea*  
(*Nerinea archimedi* d'Orbigny)



*Nerinella*  
(*Nerinea dupiniana* d'Orbigny)



*Trochalia*  
(*Nerinea grandis* Voltz)



*Ptygmatis*  
(*Nerinea bruntrutana* Thurmann)

<sup>1</sup>"*Nerinea* ..... one group, which unites the rhomboidal opening of the *Trochi* to the two canals of the mouth of *Cerithia*, thus forming a link between those genera" Sharpe, 1849, p 102.

D'Orbigny (1852) stated that changes in fold structure and the umbilicus did not correspond to overall changes in shape, also that the complex folds, used by Sharpe (1849) to define his subgenus *Prygmatis*, invariably became simple near the aperture; d'Orbigny therefore concluded that such features could not be used to subdivide the genus and rejected Sharpe's subgenera. Pictet and Campiche (1862) also regarded the subgenera as poorly defined and did not use them, although three separate genera, *Itieria*, *Nerinea* and *Cryptoplocus* Pictet and Campiche, were specified adjacent to one another within the family "Pyramidellides". The new genus *Cryptoplocus* included species which had previously been placed in *Nerinea* but which lacked folds on the columella and labrum, and had a rounded square aperture, reported to lack both an anterior canal and a posterior sinus (a selenizone would also therefore be absent). Pictet and Campiche regarded *Cryptoplocus* as intermediate between the "Pyramidellides" and "Cérithides" families; they suggested that the genus might be a connecting link between the "Cérites" and the "Nérinées".

Pictet and Campiche (1862) slightly modified the generic diagnosis for *Itieria* given by Matheron (1842), adding to it the feature of a posterior sinus at the aperture and allowing a labrum without folds. These modifications allowed them to include within *Itieria* two new "urgonien" species, which they considered to show great similarities to *Itieria cabaneti*. Gemmellaro (1863) also considered *Itieria* to be a distinct genus, probably intermediate between the "actaeonidi" and the "nerinee", similar to the former in external shape, but differing in the presence of an anterior rudimentary canal and "sinuosity" at the posterior end of the aperture. It was therefore suggested that *Itieria* was closer to *Nerinea* but that differences between the two in overall shape, growth form and apertural morphology prevented the inclusion of both types within one genus. Six new species of *Itieria* were described and, together with previously described species, these were informally divided on the basis of the presence or absence of labral folds (Gemmellaro, 1863).

Stoliczka (1867) set up a new genus *Itruvia*, which differed from *Itieria* in having a solid "twisted" columella and a short recurved canal terminating the aperture anteriorly. The four genera, *Itieria*, *Itruvia*, *Nerinea* and *Cryptoplocus*, were included in the Pyramidellidae family; Stoliczka saw great similarities between these genera and some pyramidellid groups, for example between *Itieria* and *Obeliscus*; *Cryptoplocus* and *Niso*; *Nerinea* and *Pyramidella*. Stoliczka supported the erection of *Cryptoplocus* by Pictet and Campiche (1862), but rejected the subgenera proposed by Sharpe (1850), declaring that no generic division should be based on a single character such as folds, but on all features of the shell.

#### 1.3.5 Establishment of the Nerineidae

Ooster (1869) noted the existence of forms apparently intermediate between *Nerinea* and *Itieria*, and for this reason rejected the division of the two genera stating that the boundaries between them were indistinct. *Itieria* was treated as a subgenus of *Nerinea* (Ooster, 1869). This tendency was carried further by Zittel (1873) who placed *Itieria*, *Nerinea sensu stricto*, *Cryptoplocus*, *Ptygmatis* and *Aptyxis* (all as subgenera of *Nerinea*) in the family Nerineidae Zittel (table 1.2). Zittel argued that the possession of a posterior sinus and slit band was sufficient to distinguish the Nerineidae as a distinct family belonging between the "Pyramidelliden" and the "Cerithiden". This family was characterised by the presence at the aperture of a short anterior canal; a posterior slit generating a slit band, and usually internal folds in the whorl cavity. Of these features, Zittel (1873) emphasised that the posterior sinus and slit band were the most reliable; he himself erected a subgenus, *Aptyxis* Zittel (1873) (non Troschel, 1868), which lacked internal folds; he also commented on the weakness of the anterior canal present in *Cryptoplocus*, although maintaining that a posterior slit and slit band were present in this group, contrary to the conclusions of Pictet and Campiche (1862).



FAMILY NERINEIDAE

Family	Genus	Subgenus
Nerineidae Zittel	<i>Nerinea</i> Defrance	<i>Ptygmatis</i> Sharpe
		<i>Itieria</i> Matheron (= <i>Itruvia</i> Stoliczka)
		<i>Nerinea</i> ss
		<i>Aptyxis</i> Zittel
		<i>Cryptoplocus</i> Pictet and Campiche

Table 1.1. Zittel's (1873) arrangement of the Nerineidae

Zittel (1873), because of poor definition of the group, rejected the genus *Itruvia* Stoliczka (1868), considering it to be a synonym of *Itieria*. All Sharpe's (1849) subgenera, except *Ptygmatis*, were also rejected on the basis that fold structure alone was an unsuitable parameter for subgeneric distinction. Zittel informally divided the subgenera, where appropriate (ie in *Nerinea* ss, *Ptygmatis* and *Itieria*) on the basis of fold number and umbilical character.

Zittel's *Aptyxis* was changed to *Aptyxiella* Fischer (1885) because *Aptyxis* had already been used by Troschel (1868) in a different context.

De Loriol (1886 - 88) agreed with the creation of Zittel's Nerineidae, and the groups included therein, although he considered these groups to be genera rather than subgenera. He disagreed with the use of the term *Cryptoplocus* considering it to be a synonym of *Trochalia*. Sharpe (1849) had included *Nerinea depressa* Voltz (the type species of *Cryptoplocus*) in *Trochalia*, although this action would not affect the establishment of a new and different group based on this species. The inclusion of cryptoplocid-type shells in *Trochalia* is not readily apparent from Sharpe's generic diagnosis, but it appears that the latter's concept of a columella fold included one occurring "sur la portion de la bouche qui

bouche qui recouvre le tour précédent" (Pictet and Campiche, 1862, p 257) (on the section of the whorl which covers the preceding whorl) ie the parietal wall, which was the location of the characteristic fold of *Cryptoplocus*.

In a later work, de Loriol (1890) erected the genus *Pseudonerinea*, characterised by a non-umbilicate elongate shell, with rounded whorls and a narrow oval aperture, terminated anteriorly by a canal and notched posteriorly by a long sinus which left the trace of a narrow band. This genus was considered to be close to *Pseudomelania* and *Nerinea*, although distinguished from the latter by its lack of folds.

Cossmann (1895b) considered *Pseudonerinea* to be a junior synonym of *Fibula* Piette. In a slightly earlier work (Cossmann, 1895a), the family Tubiferidae was erected containing the genus *Ceritella* Morris and Lycett and the "section" *Fibula*. The Tubiferidae was defined by the possession of a turriculate shell showing a deviated heterostrophic protoconch, overlapping whorls, no folds, an aperture notched posteriorly and subcanaliculate anteriorly. Cossmann placed the Tubiferidae among the Actaeonidae on the basis of the protoconch, the overlapping whorls and the posterior notch which he considered to be similar to features occurring in "*Cylindrites*". However in the later paper (1895b) Cossmann mentions a possible affinity between the Tubiferidae and the Nerineidae.

#### 1.3.6 Creation of the Entomotaeniata

In 1896, Cossmann published a major revision of the group in which he created a new suborder, the Entomotaeniata. This suborder was essentially characterised by both a posterior juxtasutural slit and an anterior canal at the aperture, a heterostrophic protoconch and, usually, internal folds. Three families were included in the Entomotaeniata, the Tubiferidae Cossmann (1895), the Itieriidae Cossmann (1896) and the Nerineidae Zittel (1873). An outline of Cossmann's classification including the various genera, subgenera and sections of each of these families, is given in table 1.2. Cossmann used all Sharpe's

subgenera, which had been discounted by most previous workers, and included *Cryptoplocus* as a subgenus of *Trochalia*. He also removed *Itieria* from the Nerineidae and placed it, together with *Itruvia*, in the Itieriidae which was distinguished from the Nerineidae on the basis of whorl overlap (ie the tendency for later whorls to envelop preceeding ones), a feature not shown in the Nerineidae. Cossmann (1896) was convinced that the Entomotaeniata were related to the opisthobranchs, an argument based on the heterostrophic protoconch (which had been reported only in the Tubiferidae), the occurrence of both a juxtasutural sinus and an anterior canal in some "Tectibranches", and "l'enchaînement ininterrompu qui existe ..... entre les *Actaeonidae* et les *Nerineidae*" (the uninterrupted series which exists ..... between the Actaeonidae and the Nerineidae) which presumably refers to the Itieriidae and Tubiferidae as the connecting links. Cossmann placed the Entomotaeniata between the prosobranchs and the opisthobranchs, emphasising that he considered the group to be more closely related to the latter.

SUBORDER ENTOMOTAENIATA

Family	Genus	Subgenus	Section
Tubiferidae Cossmann	{ <i>Cerithiella</i> Morris and Lycett <i>Pseudonerinea</i> de Lorient		{ <i>Fibula</i> Piette <i>Sequania</i> Cossmann
Itieriidae Cossmann	{ <i>Itieria</i> Matheron <i>Itruvia</i> Stoliczka <i>Phaneroptyxis</i> Cossmann	{ <i>Itieria</i> ss <i>Campichia</i> Cossmann	
Nerineidae Zittel	{ <i>Nerinea</i> Defrance	{ <i>Nerinea</i> ss <i>Diozoptyx</i> Cossmann <i>Ptygmatis</i> Sharpe <i>Aphanoptyx</i> Cossmann	{ <i>Acrostylus</i> Cossmann <i>Melaniptyxis</i> Cossmann
	{ <i>Nerinella</i> Sharpe	{ <i>Nerinella</i> ss <i>Bactroptyxis</i> Cossmann <i>Aptyxiella</i> Fischer	
	{ <i>Trochalia</i> Sharpe	{ <i>Trochalia</i> ss <i>Cryptoplocus</i> Pictet and Campiche <i>Endiaplocus</i> Cossmann	

Table 1.2. Cossmann's (1896) classification of the Nerineacea.

In complete contrast to Cossmann's point of view, Böhm (1900) related the Nerineidae to the Murchisoniidae on the basis of both groups possessing a sinus at the aperture and a

slit band. Böhm suggested that the presence of folds had influenced the position of the sinus, causing it to move from a central/anterior position in the Murchinsoniidae to a posterior position in the Nerineidae.

Cossmann's definitions of the genera *Nerinea* and *Nerinella* were criticised by Geiger (1901) as having indistinct limits which rendered them untenable as separate genera. Geiger also included in *Aptyxiella* some species which had previously been excluded from the group by Cossmann because they had faint columella folds. Geiger thought *Ptygmatis* showed little uniformity as a subgenus and was therefore difficult to characterise satisfactorily. He considered *Trochalia* to be so poorly defined that it was not clear whether or not it was synonymous with *Cryptoplocus*, although he recognised the latter as a well-defined subgenus. Rollier (1909) agreed with Geiger's criticism of *Nerinea* and *Nerinella*, and suggested the inclusion of *Nerinella* and its subgenera within *Nerinea*. Rollier did not consider the sinus to be of phylogenetic significance, and he therefore rejected the proposed relationship between *Murchisonia* and *Nerinea*.

Cossmann (1921) suggested that features such as columella folds and a heterostrophic protoconch occurring in both the Entomotaeniata and *Pyramidella* indicated an ancestor-descendant relationship between the two, with the posterior notch of the Entomotaeniata represented in the first pyramidellids by only a weak sinus or a protractive curve of the labrum.

### 1.3.7 Other Approaches

Dietrich (1925) in a major review of the Nerineidae family catalogued over 800 species. He apparently considered the combination of the Nerineidae, Itieriidae and Tubiferidae within the Entomotaeniata to be unjustified, firstly because other families possessing a slit were not included, and secondly the other major unifying character invoked by Cossmann, that of a heterostrophic protoconch, had been recorded only in the Tubiferidae. He also stated that overlapping whorls were found in some Nerineidae

groups (notably *Ptygmatis*); he therefore rejected the separation of the Itieriidae and the Nerineidae, considering them merely to represent two extremes of a continuum. Dietrich (1925) informally divided the Nerineidae into 5 groups:-

1 the typical *Nerinea* sl; *Nerinea*, *Acrostylus*, *Melaniptyxis*, *Fibloptyxis*, *Diozptyxis*, *Ptygmatis*, *Plesioptygmatis*, *Aphanoptyxis*, *Favria*.

2 narrowly turreted group; *Nerinella*, *Endiatrachelus*, *Bactroptyxis*, *Aptyxiella*, *Aphanotaenia*.

3 trochiform group; *Trochalia*, *Endiaplocus*, *Cryptoplocus*.

4 ovate acteonelliform group; *Itieria*, *Campichia*, *Phaneroptyxis*, *Brouzetia*, *Itruvia*, *Vernedia*, *Mrhilaia*.

5 smooth turreted group; *Pseudonerinea*, *Böhmia*.

acknowledging that this was not a natural classification.

Levasseur (1934) developed a classification of the Rauracian (Oxfordian/Lower Kimmeridgian) Nerineidae based primarily on the presence or absence of a "true" umbilicus and on the number of folds present; these groups were further subdivided on the basis of overall shape, whorl profile, ornamentation and whorl overlap. Although admitting that such a classification was artificial, Levasseur argued that it facilitated the determination of specimens.

The classification of the group given by Wenz (1940) (shown in table 1.3) basically followed Cossmann's (1896) scheme with minor modifications, such as the alteration of some names to conform with nomenclatural rules and the incorporation of groups set up after 1896. Wenz thought the superfamily Nerineacea Wenz (1940) (= Entomotaeniata

Cossmann (1896)) showed affinities with the Pyramidellacea and Opisthobranchia, but was unsure as to the closeness of the relationships involved.

Table 1.3 Wenz's (1940) classification of the Nerineacea

**SUPERFAMILY NERINEACEA [= ENTOMOTAENIATA]**

Family	Genus	Subgenus
Cerithellidae [= Tubiferidae]	<i>Ceritella</i> Morris and Lycett	<i>Ceritella</i> ss
		<i>Fibulella</i> Wenz [= <i>Fibula</i> Piette]
		<i>Sequania</i> Cossmann
	<i>?Pseudonerinea</i> de Loriol	
	<i>Böhmiola</i> Strand	
Itieriidae Cossmann	<i>Itieria</i> Matheron	<i>Itieria</i> ss
		<i>Brouzetia</i> Cossmann
		<i>Campichia</i> Cossmann
	<i>Itruvia</i> Stoliczka [= <i>Vernedia</i> Mazeran]	
	<i>?Mrhilaia</i> Pervinquière	
	<i>Phaneroptyxis</i> Cossmann	<i>Phaneroptyxis</i> ss
		<i>?Favria</i> Cossmann
	<i>?Curetia</i> Cossmann	

Family	Genus	Subgenus
Nerineidae Zittel	<i>Nerinea</i> Deshayes	<i>Nerinea</i> ss
		<i>Acrostylus</i> Cossmann
		<i>Melaniptyxis</i> Cossmann
		<i>Fibuloptyx</i> Cossmann
		<i>Diozoptyx</i> Cossmann
		<i>Ptygmatis</i> Sharpe
		<i>Laevinerinea</i> Dietrich
		<i>Teleoptyx</i> Olsson
		<i>Neoptyx</i> Pchelintsev
		<i>Plesiptygmatis</i> Böse
		<i>Gonzagia</i> Maury
		<i>Aphanoptyx</i> Cossmann
	<i>Aptyxiella</i> <sup>2</sup> Fischer	<i>Nerinoides</i> <sup>1</sup> Wenz [ <i>Nerinella</i> ]
		<i>Endiatrachelus</i> Cossmann
		<i>Bactroptyxis</i> Cossmann
		<i>Aptyxiella</i> ss
		<i>Aphanotaenia</i> Cossmann
	<i>Trochalia</i> Sharpe	<i>Trochalia</i>
		<i>Cryptoplocus</i> Pictet and Campiche
		<i>Endiaplocus</i> Cossmann

<sup>1</sup>Wenz published this replacement name because he thought that *Nerinella* had been published by Nardo, 1847, however, the ICZN have ruled that Sharpe's *Nerinella* was the first valid publication of the name; *Nerinoides* is therefore invalid (see Chapter 2)

<sup>2</sup>*Aptyxiella* was used by Wenz because of the problematic situation he perceived with *Nerinella*.



Delpy (1939) referred to the internal folds as "un caractère évolutif" and regarded them as the main criterion upon which subdivision of the family should be based. She developed a system of "grades" in which three of the genera employed by Cossmann (*Nerinea*, *Nerinella* and *Trochalia*) were used as the major categories ; within these groups the "grade" of various other genera and each described species is cited. This approach does not seem to have any phylogenetic basis or to be of use at a practical level; it has not been adopted to any significant extent by other workers. Delpy suggested elongate Pleurotomariidae were ancestors of the Nerineidae, which in turn gave rise to the Campanilidae.

In the preparation of the Nerineacea section of the Treatise, Cox (manuscript circa 1953) followed Cossmann's tripartite division of the group and simply lists published genera within these, although in the Nerineidae the genera were informally divided firstly on the basis of fold number and secondly on umbilical character.

Tiedt (1958) discussed the problems involved in dividing the Nerineidae at generic and subgeneric levels and concluded that fold structure was a relatively constant character and was therefore more useful for taxonomic purposes than external shape and ornament, both of which may have been influenced by local ecological factors.

Taylor and Sohl (1962) resurrected the term Entomotaeniata for an order including the superfamilies Nerineacea and Pyramidellacea after Cossmann (1921). Within the superfamily Nerineacea were included the families Ceritellidae, Nerineidae, Nerinellidae Pchelintsev (1960) and Itieriidae.

### 1.3.8 Latest Ideas

The most recent review of nerineid taxonomy was presented by Pchelintsev (1965 in Russian; 1968 in English) who raised the three major groupings of Cossmann to superfamily status and also separated the Nerinellacea as a superfamily distinct from the

Nerineacea. The taxonomic divisions within these superfamilies are outlined in table 1.5. Pchelintsev increased the number of genera considerably, erecting many new ones, and including some which had been proposed in earlier publications (Pchelintsev, 1925; 1931; 1934; 1954). The four superfamilies Tubiferacea, Nerineacea, Nerinellacea and Itieriacea were included in the order Murchisoniata together with the Murchisoniacea, Procerithiacea, Cerithiacea, Turritellacea and Scalacea.

Pchelintsev considered the Murchisoniata were characterised by oval, conical or turreted shells, with, at the aperture, an anterior siphonal notch or canal and a notch in the lateral surface. This notch was, for Pchelintsev, a major unifying character of the order; he also considered that a "direct succession in the general type of shell and form of aperture" (page 1, 1968) existed between the Palaeozoic Murchisoniacea and the earliest Mesozoic families, and that the latter were continuations of "phylogenetic branches within the superfamily Murchisoniacea during the Paleozoic" (page 2). Thus Pchelintsev considered that both the Tubiferacea and the Nerineacea arose directly from the Murchisoniidae during the Triassic; that the Nerinellacea developed from the Hormotomidae, which diverged from the Murchisoniidae in the Cambrian, and that the Itieriacea arose via the Pithodeidae, which split off from the Murchisoniidae in the Cambrian slightly before the Hormotomidae divergence.

Table 1.4 Pchelintsev's (1968) classification of the Nerineacea

MURCHISONIATA PCHELINTSEV

Superfamily	Family	Genus
Tubiferacea Cossmann	Ceritellidae Wenz	<i>Fibula</i> Piette <i>Sequania</i> Cossmann
	Pseudonerineidae Pchelinsev	<i>Pseudonerinea</i> Loriol <i>Pseudonerinella</i> Pchelintsev

Superfamily	Family	Genus
Itieriacea Pchelintsev	Phaneroptyxisidae Pchelintsev	<i>Phaneroptyxis</i> Cossmann
		<i>Pentaptyxis</i> Pchelintsev
		<i>Tetraptyxis</i> Pchelintsev
	Itieriacea Pchelintsev	<i>Itieria</i> Matheron <i>Campichia</i> Cossmann
Nerineacea Wenz	Fibuloptyxidae Pchelintsev	<i>Melaniptyxis</i> Cossmann
		<i>Fibuloptyx</i> Cossmann
	Nerineidae Zittel	<i>Nerinea</i> DeFrance (subgenera <i>Nerinea</i> ss and <i>Paleonerinea</i> Pchelintsev)
		<i>Turbinea</i> Pchelintsev
		<i>Funiptyxis</i> Pchelintsev
		<i>Cossmannea</i> Pchelintsev
		<i>Acrostylus</i> Cossmann
		<i>Sculpturea</i> Pchelintsev
		<i>Salinea</i> Pchelintsev
		<i>Archimedeia</i> Pchelintsev
		<i>Etallonea</i> Pchelintsev
	Ptygmatisidae Pchelintsev	<i>Aphanoptyx</i> Cossmann
		<i>Fibuloptygmat</i> Pchelintsev
		<i>Ptygmatis</i> Sharpe
		<i>Trochoptygmatis</i> Pchelintsev
		<i>Scalaepygmatis</i> Pchelintsev
		<i>Megaptyxis</i> Pchelintsev
		<i>Endiaplocus</i> Cossmann

Superfamily	Family	Genus
Nerinellacea Pchelintsev	Cryptoplocusidae Pchelintsev	<ul style="list-style-type: none"> <li><i>Cryptoplocus</i> Pictet Campiche</li> <li><i>Conoplocus</i> Pchelintsev</li> </ul>
	Diptyxisidae Pchelintsev	<ul style="list-style-type: none"> <li><i>Diptyxis</i> Oppenheim</li> <li><i>Cylindroptyxis</i> Pchelintsev</li> </ul>
	Diozoptyxidae Pchelintsev	<ul style="list-style-type: none"> <li><i>Umbonea</i> Pchelintsev</li> <li><i>Neoptyxis</i> Pchelintsev</li> <li><i>Diozoptyxis</i> Cossmann (emend Pchelintsev)</li> </ul>
	Nerinellidae Zittel (emend Pchelintsev)	<ul style="list-style-type: none"> <li><i>Nerinella</i> Sharpe [= <i>Nerinoides</i> Wenz]</li> <li><i>Aptyxiella</i> Fischer</li> <li><i>Contortella</i> Pchelintsev</li> </ul>
	Elatoriellidae Pchelintsev	<ul style="list-style-type: none"> <li><i>Elatoriella</i> Pchelintsev</li> <li><i>Crimella</i> Pchelintsev</li> </ul>
	Bactroptyxisidae Pchelintsev	<i>Bactroptyxis</i> Cossmann
	Elegantellidae Pchelintsev	<ul style="list-style-type: none"> <li><i>Elegantella</i> Pchelintsev</li> <li><i>Aplocus</i> Pchelintsev</li> <li><i>Valanginella</i> Pchelintsev</li> </ul>
	Auroraellidae	<ul style="list-style-type: none"> <li><i>Auroraella</i> Pchelintsev</li> <li><i>Endiatrachelus</i> Cossmann</li> </ul>
	Upellidae Pchelintsev	<ul style="list-style-type: none"> <li><i>Florella</i> Pchelintsev</li> <li><i>Upella</i> Pchelintsev</li> <li><i>Tauricella</i> Pchelintsev</li> </ul>

Superfamily	Family	Genus
	Polyptyxisidae Pchelintsev	<i>Polyptyxis</i> Pchelintsev <i>Polyptyxisella</i> Pchelintsev <i>Balkanella</i> Pchelintsev
	Triptyxisidae Pchelintsev	<i>Triptyxis</i> Pchelintsev <i>Multiptyxis</i> Pchelintsev

Djalilov (1975) noted that "Murchisoniata" had been used by Cox and Knight (1960) for a suborder comprising of only the superfamily Murchisoniacea, and concluded that Pchelintsev's (1965) use of the term was therefore invalid. Djalilov also criticised the combination of the 4 superfamilies, Tubiferacea, Nerineacea, Nerinellacea and Iteracea, with the Murchisoniacea arguing that the latter group lacked a siphonal canal, internal folds, sutural ramps and also had an apertural shape different to those occurring in the former groups. In addition, Djalilov considered that the contrast between the medially placed sinus in the Murchisoniacea and the posterior juxtasutural sinus in the nerineids demonstrated important anatomical differences between the two. Furthermore, the association of the Procerithiacea, Cerithiacea, Turritellacea and Scalacea with the four nerineid superfamilies was rejected as the former groups showed different apertural morphologies and also lacked internal folds (Djalilov, 1975). However, the systematic unity of the nerineids was accepted and Djalilov used the term "Entomotaeniina [nom. correct. hic (pro Entomotaeniata Cossmann, 1896)]" (p 27) for a suborder which included the four superfamilies. Djalilov regarded the siphonal canal and anal notch of the nerineids as sufficient evidence for their placement in the "monobranchial Prosobranchia" (p 26), noting that a heterostrophic protoconch had been reported only in an "atypical genus, *Pseudonerinea*" (p 26).

Barker (1977) considered that the presence of a slit and selenizone in the Nerineacea indicated archaeogastropod affinities (by comparison with the Pleurotomariacea and the

Murchisoniacea), whereas the rudimentary siphonal canal indicated a separation of inhalent and exhalent currents, characteristic of the caenogastropods. He therefore concluded the Nerineacea were a primitive superfamily of the Caenogastropoda which retained some archaeogastropod features, and that suggested affinities with the opisthobranchs were unjustified. Barker also considered Pchelintsev's erection of the Murchisoniata totally unjustified and criticised many of Pchelintsev's families and genera as being poorly defined and ambiguous.

## CHAPTER 2

### **SYSTEMATICS**

#### **2.1 INTRODUCTION**

This chapter consists of a taxonomic review of the Cretaceous nerineid fauna encountered during the present study. Material has been collected from localities in France, Portugal, Austria and Spain. The specimens obtained come from various sediments and palaeoenvironments which are discussed in Chapter 4. Good stratigraphic control was available in the majority of cases. This material is now part of the British Museum (Natural History) Collection (BM(NH) GG21830 - 22112).

Specimens within various museum collections have also been studied; location details and numbers, together with collection locality and stratigraphic horizon are given where appropriate. Some species are known exclusively from museum collections and are redescribed here when the material has been used for the basis of other research and some taxonomic consideration has been deemed necessary.

Where appropriate, problems at subfamily, generic and specific level have been discussed. The majority of the pre-existing species are reported for the first time since the beginning of this century; where appropriate, complete diagnoses, descriptions, figures and plates have been given to clarify previous inadequate accounts or to support new interpretations.

Details concerning stratigraphic range and localities, together with the raw statistical data used in the analyses, are given in the appendices.

## 2.2 MEASURED PARAMETERS

There are only a limited number of parameters which can be readily measured on nerineid shells. The specific descriptions below include, as far as possible, average values of four parameters which reflect the actual morphology present and therefore allow consistent quantitative description of species. The separation of taxa which can be achieved using these measurements has been analysed graphically in *Eunerinea* and *Pchelinsevia*.

The parameters used provide, in the opinion of the author, the most consistent and accurate measures of various aspects of nerineid shell morphology. Apical angle, sutural angle and, to a lesser extent, h/w ratio have been used by many other workers (eg d'Orbigny, 1843; Pictet and Campiche, 1862; Cossmann, 1907; Delpey, 1939); whorl concavity index has been used only recently (Wieczorek, 1979). Analysis of the resolution that can be achieved using apical angle, sutural angle and h/w ratio (in relation to high-spired nerineids) has shown that apical angle gives the best separation of species, followed by sutural angle and h/w ratio, which are of approximately equal use (Barker, 1976). However, the material covered here includes a variety of shell shapes, from *Nerinella* to *Phaneroptyxis*, with some groups clearly showing non-isometric growth; it therefore seems likely that sutural angle, h/w ratio and whorl concavity index provide more reliable results.

The methods used to obtain the measurements are outlined diagrammatically in figure 2.1 and discussed below.

It should be emphasised that the quality and quantity of the material available precludes any claim for these figures to represent definitive values for the species concerned. The average values (and ranges) should be used as guides, not as absolutes.

It is not always possible to measure all four parameters on each shell. When plotting scatter graphs of two measurements these have to come from the same fossil which



means that the number of points on the graphs may be lower than the number of measurements given in the text. The figures used are from individual shells.

### 2.2.1 Apical Angle

This has been one of the most widely used parameters in quantitative species diagnosis.

The apical angle is typically a small numerical value (under 30°); it is closely linked to overall morphology - a low apical angle indicates a slender elongate shell, whereas a high one reflects a stoutly conical shape. Even relatively small differences in apical angle can result in profound differences in shell form.

Some species show markedly anisometric growth, which means that the "apparent" apical angle changes with growth, sometimes appearing to "increase" (eg some specimens of *D. cochleaeformis*, section 2.16), sometimes apparently decreasing (eg *E. chloris*, when shell growth becomes cylindrical). In addition, other shell features such as bulging sutural ramps or convex whorl profile can affect the apical angle value so that two species with similar overall shell shape can have rather different apical angles. It can therefore be difficult to obtain accurate results for this parameter. The effect of whorl morphology on apical angle cannot be eliminated without reducing the measurement to a theoretical one. Changes in apical angle during growth mean that only shells where the early whorls are present should be used. In this study, the apical angles given were measured from the first 50 mm of reasonably complete shells; the resulting values range from 7° to 28°.

The inherent inaccuracies likely in apical angle measurement make it a relatively unreliable parameter for use below generic level. Species within a single genus tend, in any case, to have similar shell shapes (there are exceptions to this eg *E. gigantea*) and therefore similar apical angles, so that the use of this parameter for species resolution is likely to be limited.

### 2.2.2 Sutural Angle

Sutural angle is relatively easy to measure, it does not appear to change significantly during ontogeny, is not affected by external morphology and appears to give reasonable species resolution (own results; Barker, 1976).

The angle is obtained from longitudinal axial sections of shells. It is the obtuse angle formed between the coiling axis of the shell (which runs centrally down the length of the shell in nerineids) and a line joining two points on the suture which are 180° (ie half a whorl) apart (see figure 2.1).

The sutural angle can be quoted as the acute angle formed (eg Delpy, 1939); the obtuse angle is used here because it directly reflects the differences in morphology, the greater the angle, the more oblique the suture line between whorls. A theoretical sutural angle of 90° indicates a near horizontal suture, with very little movement along the coiling axis for each whorl revolution. The sutural angles recorded here lie between 92° and 117°.

### 2.2.3 h/w Ratio

This parameter is the whorl height (measured perpendicular to whorl width, between two successive whorl widths) divided by the larger whorl width (measured between two suture points 180° apart - see figure 2.1). Median longitudinal sections are usually required.

All the nerineids encountered in this study have a whorl width greater than whorl height; the h/w ratio is therefore consistently a decimal figure below 1. This facilitates easy comparison; the nearer the h/w ratio to 1, the more elongate, narrower and high whorled the shell. A low h/w ratio indicates a squat and wide shell with low whorls. The values given here range from 0.39 to 0.71.

In some cases w/h ratios have been quoted (eg Barker, 1976), but the use of h/w gives a range of values which are more readily interpreted and compared.

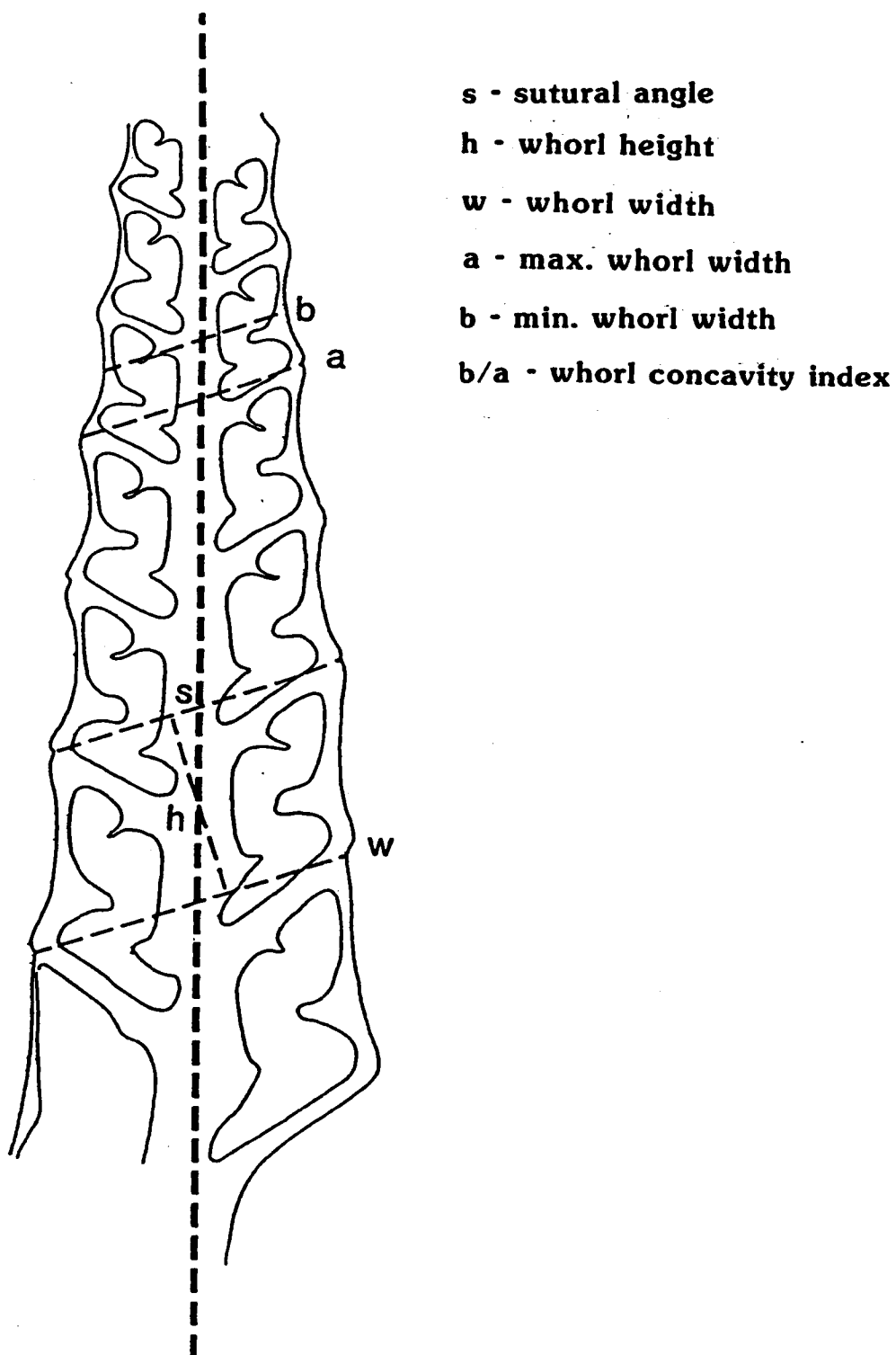


Figure 2.1 Median longitudinal section of *Eunerinea* to demonstrate derivation of the quantitative parameters given in species descriptions.

#### 2.2.4 Whorl Concavity Index

The whorl concavity index is computed by dividing the "minimum" whorl diameter, (usually occurring at mid-whorl) by the "maximum" whorl diameter (at the whorl suture) within a single whorl revolution (see figure 2.1). Measurements can be made on whole or sectioned specimens.

A whorl concavity index of 1 indicates a totally flat whorl profile; below 1 shows a concave profile, the degree of concavity being greater the lower the decimal. This is the most common state in the nerineids, for example the values given here for concave-whorled shells range from 0.63 to 0.87. Convex whorls give a figure above 1; this is quite unusual in nerineids, but does occur eg *Phaneroptyxis africurgonia* Dietrich (section 2.22.1) has a whorl "concavity" index of 1.21, indicating that its whorl profile bulges out between sutures.

#### 2.2.5 SYNONYMY SIGNS

The following synonymy signs have been used before publication dates (Matthews, 1973):-

- \*           with this publication, species becomes valid
- .           author accepts responsibility for attaching this reference to the species
- No sign   author has no right to accept responsibility for attaching this reference to the species but has no cause to doubt the allocation
- ?           allocation of reference to this species is subject to some doubt

- (?) reference probably applies to this species but the author cannot be certain
- p. reference applies only in part to this species
- v author has checked the deposited specimens referred to in this reference
- v. due to evidence of deposited specimens, author takes responsibility for assignment of this reference to this species
- v\* author has seen the type of the species

## 2.3 Class *GASTROPODA*

### Subclass *OPISTHOBRANCHIA*

#### Discussion

The inclusion of the Nerineacea within the Opisthobranchia follows the discovery of heterostrophic protoconchs in two nerineacean families, Nerineidae (*Diozoptyxis*) and Nerinellidae (?*Polyptyxisella*). The implications of these protoconchs for the systematic placement of the Nerineacea in higher gastropod taxonomy are discussed in Chapter 6.

### Order ENTOMOTAENIATA Cossmann

#### Discussion

This order was erected by Cossmann in 1896 to include the families Nerineidae, Itieriidae and Ceritellidae (= Tubiferidae). Another family has since been distinguished, the Nerinellidae (Pchelintsev, 1968). The Nerineacea are considered to be sufficiently separated phylogenetically from other primitive opisthobranch groups to merit a separate order.

Cossmann (1921) later suggested that the pyramidellids were descended from the nerineids. This led to the inclusion of both superfamilies (Nerineacea and Pyramidellacea) within the Order Entomotaeniata (Taylor and Sohl, 1962). The differences which separate these two groups are discussed in Chapter 6, and it is concluded that they are not closely related. The author considers that the Order Entomotaeniata should include only the four nerineid families (Nerineidae, Itieriidae, Ceritellidae and Nerinellidae) and that the superfamily Pyramidellacea belongs to a distinct and separate order.

Pchelintsev's (1968) erection of the "Murchisoniata" as an order is rejected. The author does not agree that the component superfamilies (Murchisoniacea, Tubiferacea, Nerineacea, Nerinellacea, Itieriacea, Procertithiacea, Cerithiacea, Turritellacea, Scalacea) in any way represent a single phylogenetic unit. Pchelintsev's use of the name "Murchisoniata" is invalid, due to prior use by Cox and Knight (1960).

### Superfamily **NERINEACEA** Wenz

#### Discussion

The composition of the Order Entomotaeniata given here, strictly speaking, obviates the need for a superfamilial term. However, the name is widely used.

Pchelintsev (1968) has raised the three pre-existing nerineid families to superfamilies, and added a fourth. This action is not supported by scientific or taxonomic argument, and appears to merely a device designed to allow the creation of numerous new "families". Herein, the four nerineid major groupings are retained as families as the systematic separation which they show does not appear to merit superfamilial status. Pchelintsev's "families", where considered to represent true phylogenetic groups, are cited as subfamilies. Lysenko and Aliyev (1987) also propose a new "family", the concept of which is accepted, but again it is regarded as a subfamily for the reasons given above.

Some genera are recorded as "Incertae subfamiliae" (after Matthews, 1973). In these cases there is no known subfamily which offers a satisfactory systematic grouping for the genus.

## Family **NERINEIDAE** Zittel

### 2.4 Genus *Nerinea* Deshayes, 1827

[= *Fibloptygmatis* Pchelintsev, 1965<sup>1</sup>]

Type species. By monotypy, *Nerinea mosae* Deshayes, 1827

#### Discussion

The first valid publication of *Nerinea* appears to have been made by Deshayes (1827), although Defrance described a new genus "Nérine" in 1824 and "Nériné" in 1825, in the latter case a figure of "Nériné tuberculeuse" accompanied the description. Although earlier workers accepted Defrance's authorship of the genus (d'Orbigny, 1843; Conrad, 1852; Pictet and Campiche, 1862 etc), some later authors (Wenz, 1940; Cox, 1949; Barker, 1976) have regarded Deshayes (1827) as author of the genus. However, Pchelintsev (1968) and Calzada (1986) cite "*Nerinea* Defrance (1825)". This problem regarding original authorship of the genus *Nerinea* has been discussed by Cox (1949) and Barker (1976). "Nérine" and "Nériné" are both French vernacular names which are not considered to represent scientific names, and are therefore not valid (ICZN, 1985, Articles 11(b), 12(c) and p 272).

The main importance of resolving the authorship of *Nerinea* lies in determining the type species of the genus, and thus the defining features of the latter. It seems clear that ICZN rules preclude Defrance's names, and that *Nerinea* Deshayes is valid. The type

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<sup>1</sup>Pchelintsev published a major review of nerineid taxonomy in 1965, in Russian. This was translated into English and published in 1968. The dates given for Pchelintsev's taxonomic actions in this work are therefore 1965, as this is the date they were first published, however, any discussion of Pchelintsev's actions is related to the 1968 publication, as it is only this publication which can be read by the author.



species of *Nerinea* is therefore, by monotypy, *Nerinea mosae* Deshayes<sup>1</sup> which is described by Deshayes (1827) and later figured (Deshayes, 1831 - see figure 2.2). *N. mosae* is a stoutly conical shell, with concave whorls and bulging sutural ramps<sup>2</sup>. The whorl cross-section shows the fold formula 2,1,1,1 and the shell appears to be narrowly umbilicate, although this is never categorically stated and is not clear from the engraving (Deshayes, 1831).

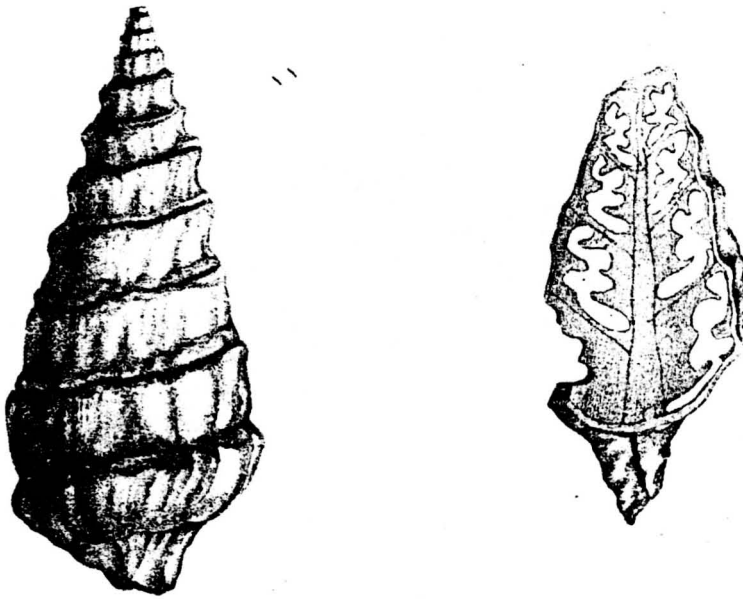


Figure 2.2 *Nerinea mosae* Deshayes - the first valid *Nerinea* species. After Deshayes (1831).

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<sup>1</sup> Misprinted "*Nerina*" in the species heading (Deshayes, 1827, p 535).

<sup>2</sup>"elle est pyramidale ..... les tours de spire ..... sont creusés en gouttière transversalement; la suture est placée sur l'endroit le plus saillant de chaque tour" Deshayes 1827, p 535

Several authors have discussed species which are very similar to *N. mosae* and appear to belong to the same genus (Pchelintsev, 1968; Wieczorek, 1975; Barker, 1976). These species are relatively few in number; *N. costulata* Etallon (Pchelintsev, 1968), *N. diozptygmatis* Delpy (Wieczorek, 1975), *N. schiosensis* Pirona, *N. nobilis* Münster and *N. requieni* d'Orbigny (Barker, 1976). Earlier suggestions associating *N. mosae* with *Itieria* species (Zittel, 1873; de Loriol, 1886-88 and 1889-92) or *Ptygmatis* species (Cossmann, 1898; Dietrich, 1925; Cox, 1949) appear to have been unsatisfactory (Pchelintsev, 1968; Barker, 1976). *N. mosae* and its related species therefore form a small genus which must, by nomenclatural rules of priority, be called *Nerinea*..

The genus "*Fibloptygmatis* " erected by Pchelintsev (1968), with the type species *N. mosae* must be regarded as an objective junior synonym of *Nerinea*. Both Wieczorek (1975) and Barker (1976) consider *Nerinea* to be close to *Phaneroptyxis*, although fold patterns clearly separate the two genera.

## 2.5 "*Nerinea sensu stricto*"

The acceptance by earlier workers of Defrance's authorship of *Nerinea* resulted in interpretations of the genus based on the characters of "*Nériné tuberculeuse*" (Sharpe, 1849; Pictet and Campiche, 1862). However, in other cases, any shells which could be regarded as "nerineids" in the most general sense were listed as belonging to the genus *Nerinea* (Voltz, 1836; d'Orbigny, 1843 and 1852; Conrad, 1852). Cossmann (1896) attempted to regularise the situation by listing "*Nerinea* Defrance" with a very loose definition (eg fold number 1 to 7; folds simple or complex) and then defining "*Nerinea sensu stricto*" with the type species "*N. tuberculosa* Defrance", although Defrance had not used this non-vernacular name. The generic diagnosis was not however based on *N. tuberculosa* as figured by Defrance; Cossmann did not have access to Defrance's type specimen (which he recorded as lost) and considered that Defrance's figure of the species was inaccurate in respect of fold number. Cossmann's "*Nerinea sensu stricto*"

was described as having elongate shells with concave whorls and a h/w ratio of 0.66 or less (2/3:1). Internally the shell was non-umbilicate with 3 simple folds (1,1,1,0).<sup>1</sup> This definition of *Nerinea* ss was accepted by later workers (Dietrich, 1925; Wenz, 1940).

## 2.6 Genus *EUNERINEA* Cox, 1949

[= *Archimedeia* Pchelintsev, 1965]

Type species. By original designation, *Nerinea castor* d'Orbigny, 1847

### Diagnosis

"Shell of medium acuteness, with strongly concave whorls and a convex, projecting sutural region. Aperture rhomboidal, not greatly extended anteriorly, where it ends in a short canal; with three internal folds - one on the labrum, one on the columella and one on the parietal wall" Cox, 1949, p 250.

### Discussion

Cox (1949) pointed out that Cossmann's use of the name *Nerinea* with the type species *N. tuberculosa* was unacceptable since it clearly contravened nomenclatural laws of priority. A new subgenus, *Eunerinea* Cox was proposed which largely, though not entirely, conformed to Cossmann's concept of *Nerinea* ss apart from "dernier tour atteignant parfois le quart de la longueur totale" (Cossmann, 1896, p 26) (last whorl sometimes reaching a quarter of the total length).

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<sup>1</sup>"Forme un peu trapue; spire a galbe conique parfois assez allongee; tours excaves, dont la hauteur n'atteint pas ou ne depasse guere les deux tiers de la largeur ..... non-ombiliquee; un pli a la columelle, un pli parietal, un pli au labre, tous trois lamelleux et simples" Cossmann, 1898, p 25 - 26.

Cox's proposal of *Eunerinea* appears to be an eminently appropriate and satisfactory resolution of the *Nerinea* and "*Nerinea* ss" problem. Pchelintsev's (1968, page 9) reasons for rejecting Cox's suggestions do not appear to fully consider nomenclatural rules and show an incomplete appreciation of the situation. Wieczorek (1975, page 158) accepts Cox's arguments, but rejects the proposed taxonomic amendments apparently on the basis of insufficient knowledge and the inconvenience such changes would cause. Neither of these reasons are valid grounds for rejecting the taxonomic amendments suggested by Cox.

Pchelintsev (1968, p 14) erected a new genus "*Archimedeia*" (type species *Nerinea archimedi* d'Orbigny, 1843) which conformed to the generic diagnosis of *Eunerinea* (almost equivalent to *Nerinea* ss (sensu Cossmann). Pchelintsev distinguished this genus on the basis of higher whorls, smoother sutural ramps and only poorly developed external ornament. However, the group is not well characterised; eight species were listed as belonging to the group, only two of which occur outside the Crimean-Caucasian region and are not species erected by Pchelintsev. Pchelintsev does not offer any quantitative definition of "high whorled" (eg "typical" sutural angles or h/w ratios); the other features he mentions are not commonly used to make generic distinctions within the Nerineacea and are often affected by the quality of preservation. Any qualitative approach to identifying "*Archimedeia*" species would appear to be extremely difficult judging from the information available (see Pchelintsev, 1965, plate 15, figures 3 and 4; plate 16, figures 1, 2 and 3).

It is true that some *Eunerinea* species have higher whorls than others (see the discussion of *E. archimedi* and *E. vogtiana* on section 2.8.3) but it appears that the benefit gained by separating such species (which may or may not represent a separate phylogenetic trend) is rather minimal, particularly as confusion is likely to result from the poorly defined criteria upon which distinction would be based. The present study has therefore retained *N. archimedi* within *Eunerinea* and "*Archimedeia*." is considered to be a subjective junior synonym of *Eunerinea*.

## 2.7 Genus *Cossmannea* Pchelintsev, 1931

Type species. By original designation, *Nerinea desvoidyi* d'Orbigny, 1852.

### Discussion

Cox considered that as *Cossmannea* Pchelintsev differed from *Eunerinea* only in fold number, the former possessing two internal folds (1,0,1,0), the latter three (1,1,1,0), the two groups should be included in the same genus, which would have to be *Cossmannea* (due to priority rules as *Cossmannea* was established earlier) with *Eunerinea* as a subgenus.

However, Cox's inclusion of *Cossmannea* and *Eunerinea* in the same genus do not appear to be justified. There is no consensus as to which nerineid characters should be used as a basis for generic definition. Indeed, much of the classification of the Nerineaceae, based on various and different characters depending on the predilections of individual workers, has resulted in widely diverging ideas on how the group should be split, particularly at generic level. In such a situation, an approach which keeps generic groups independent of each other until true phylogenetic characters are resolved would seem to be most appropriate. In the case of *Eunerinea* and *Cossmannea*, the difference in fold number is significant; also Barker (1976) notes that *Cossmannea* species always have a higher h/w ratio than *Eunerinea*. There are, therefore, adequate grounds for considering the two groups to be two distinct genera albeit closely related ones.

## 2.8 Genus *EUNERINEA* Cox, 1949

Type species. By original designation, *Nerinea castor* d'Orbigny, 1847.

### 2.8.1 *EUNERINEA ARCHIMEDI* d'Orbigny

(Figures 2.3a, b, c<sup>1</sup>)

\*1843 *Nerinea archimedi* d'Orbigny, p 78, 79, plate 158, figures 3 and 4.

1862 *Nerinea archimedi* d'Orbigny; Pictet and Campiche, p. 249, 251.

p.1907 *Nerinea vogtiana* de Mortillet, Cossmann, plate 3, figure 2 only.

(?)1916b *Nerinea archimedi* d'Orbigny; Cossmann, p 350.

.1962 *Nerinea vogti* de Mortillet var. *archimedi* d'Orbigny; Benkőné-Czabaly,  
plate 3, figures 3 and 4.

#### Diagnosis

Narrowly tapering shell, tending towards cylindrical shape in later ontogeny. High whorls showing a moderately concave whorl profile and moderate to weak sutural ramps which have delicate crenulated ornament (not sufficiently developed to form discrete tubercles). Relatively high, elongate whorls, which give rise to a large sutural angle.

#### Material

BM(NH) GG 21862 - 21869

Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris B14762

Collection Curet, Laboratory of Invertebrate Palaeontology, Université de Paris VI

(Pierre et Marie Curie), drawer 7155

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<sup>1</sup>Bar represents 10 mm.

### Horizons and Localities

Upper Hauterivian, Silicified Locality, S of Crismina, Sintra Area, Portugal. Upper Barremian, Orgon, Brouzet and Calissane Chateau, S of France.

### Description

There is a strong, thick, solid columella (ie non-umbilicate). The whorl cross-section is an elongate rectangle. The typical generic fold arrangement is present, consisting of 3 simple strong folds (1,1,1,0). This species is more slender and higher whorled than many in the genus; it also shows less prominent sutural ramps than are typical.

### Measurements

Apical angle: 14° (range 13° - 14°, N = 3)

Sutural angle: 112° (range 107° - 117°, N = 5)

h/w ratio: 0.57 (range 0.55 - 0.60, N = 4)

Whorl concavity index: 0.79 (range 0.70 - 0.83, N = 6)

### Occurrence

*E. archimedi* has been described from France (d'Orbigny, 1843), Algeria (Coquand, 1862), and Hungary (Benkőné-Czabaly, 1962); the present study collected this species in southern France and Portugal (locality numbers: 7, 17, 25, 45 see appendix 1).

### Stratigraphic Range

In western Europe the species is found in Upper Hauterivian to Upper Barremian strata; in Hungary it is described from Albian deposits (Benkőné-Czabaly, 1962).

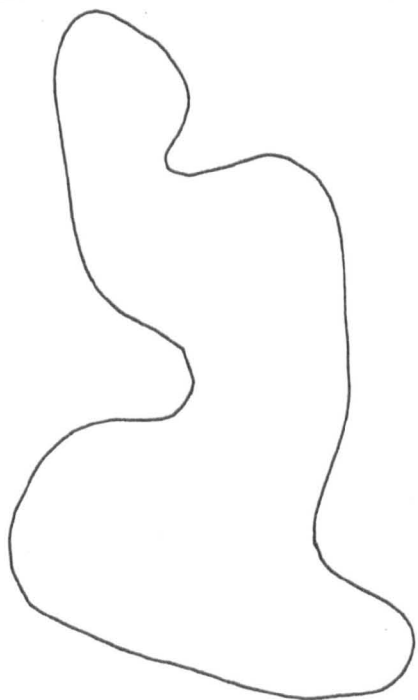
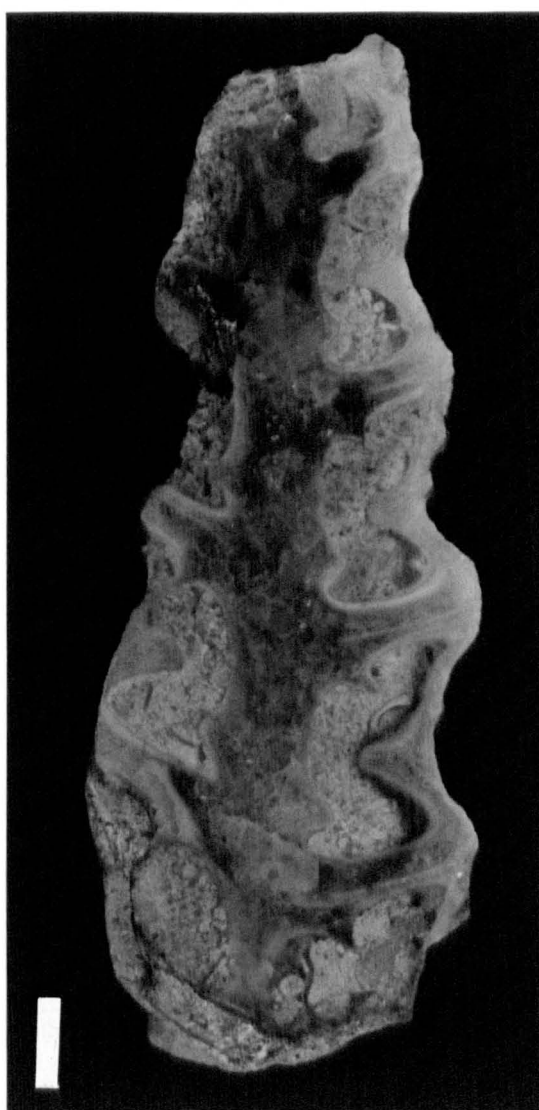
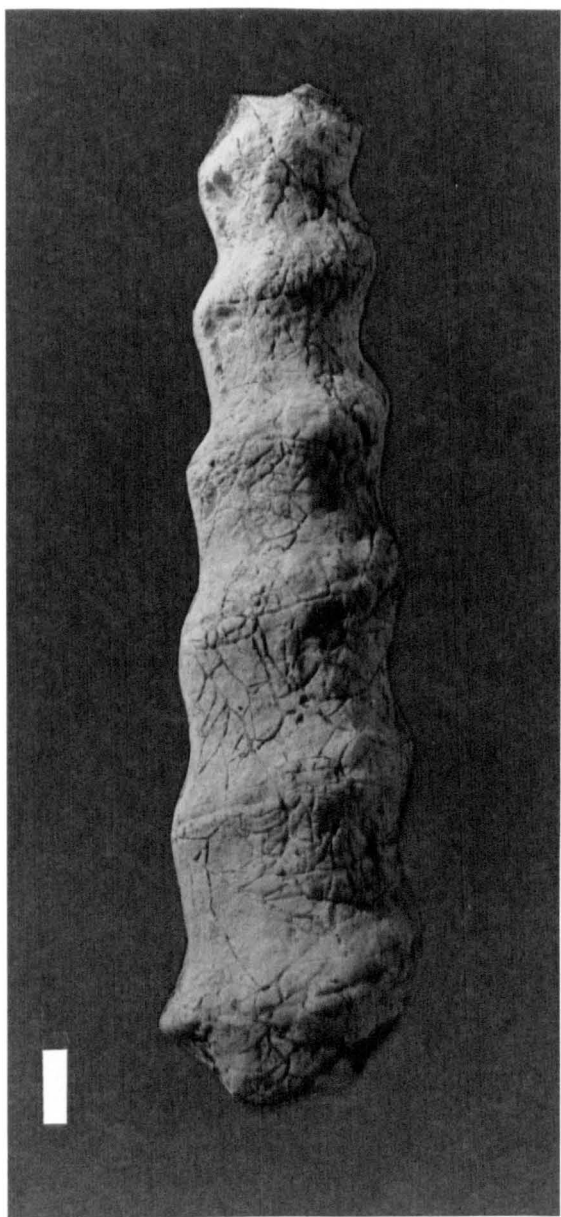


Figure 2.3a *Eunerinea archimedi* d'Orbigny. External morphology. BM(NH) GG21862. Upper Barremian, Orgon, France.

Figure 2.3b Internal morphology. BM(NH) GG21863. Upper Barremian, Calissane Chateau, France.

Figure 2.3c Fold pattern in single whorl section. BM(NH) GG21865. Upper Barremian, Calissane Chateau, France. Actual whorl height = 20 mm



## 2.8.2 *EUNERINEA VOGTIANA* de Mortillet, 1856

(Figures 2.4)

- \*1856 *Nerinea Vogtiana* de Mortillet, p71<sup>1</sup>
- 1857 *Nerinea Vogtiana* de Mortillet, p 43, 44
- v.1862 *Nerinea Vogtiana* Mortillet; Pictet and Campiche, p 240, 241, plate 68, figures 1 and 2
- p.1907 *Nerinea vogtiana* de Mortillet; Cossmann, p 10, 11, 12, text figure 2, plate 3, figures 1 and 4 (not figures 2 and 3)
- 1916a *Nerinea vogtiana* de Mortillet; Cossmann, p 14, plate 1, figure 29.
- 1916b *Nerinea vogtiana* de Mortillet; Cossmann p 349, 350, plate 10, figures 15 and 16.
- 1965 *Cossmannea (Eunerinea) vogtiana* (de Mortillet); Rossi Ronchetti, p 253 - 255, plate 39, figures 3 and 4.

### Diagnosis

Narrowly conical shell, approaching cylindrical as size increases. Salient and wide sutural ramps, bearing pronounced tubercular ornament. Pronounced whorl concavity.

### Material

BM(NH) GG 21870 - 21893

Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris B14761

Museum d'Histoire Naturelle de Geneve, Geneva AIII - 101 - 14317

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<sup>1</sup>I have been unable to locate the type material of De Mortillet, who did not figure this species. Pictet and Campiche's interpretation of *E. vogtiana* has therefore been followed.

### Horizons and Localities

Upper Hauterivian, Silicified Locality, S of Crismina, Sintra Area, Portugal. Upper Barremian, Orgon, Calissane Chateau, S of France. "Urgonian", Orgon and Annecy, France.

### Description

This species is a typical member of the genus, except perhaps in the conical shape which is shown in early/intermediate stages of ontogeny. Internally there is a strong, thick solid columella, a moderately elongate rectangular whorl cross-section which shows a 1,1,1,0 fold pattern consisting of strong simple folds (see figure 2.4c).

### Measurements

Apical angle :  $16^{\circ}$  (range  $15^{\circ}$  -  $17^{\circ}$ , N = 3)

Sutural angle :  $107^{\circ}$  (range  $100^{\circ}$  -  $112^{\circ}$ , N = 6)

h/w ratio : 0.50 (range 0.47 - 0.53, N = 4)

Whorl concavity index : 0.70 (range 0.67 - 0.73, N = 6)

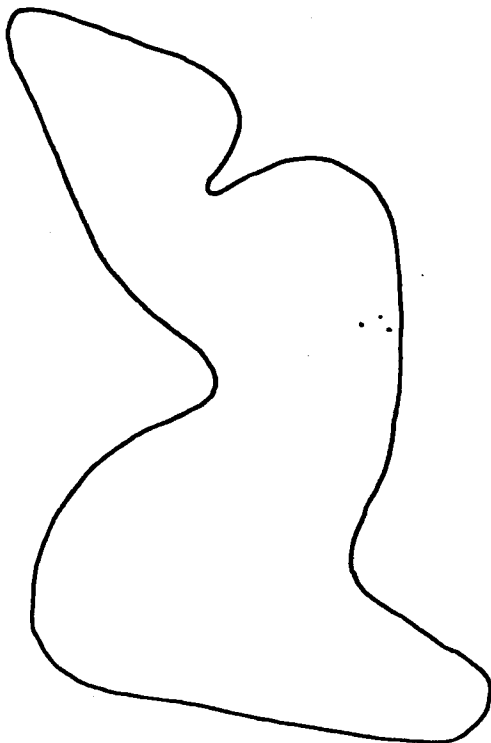


Figure 2.4c *Eunerinea vogtiana* (de Mortillet). Fold pattern in single whorl section. BM(NH) GG21873. Upper Barremian, Calissane Chateau, France. Actual whorl height = 20 mm.

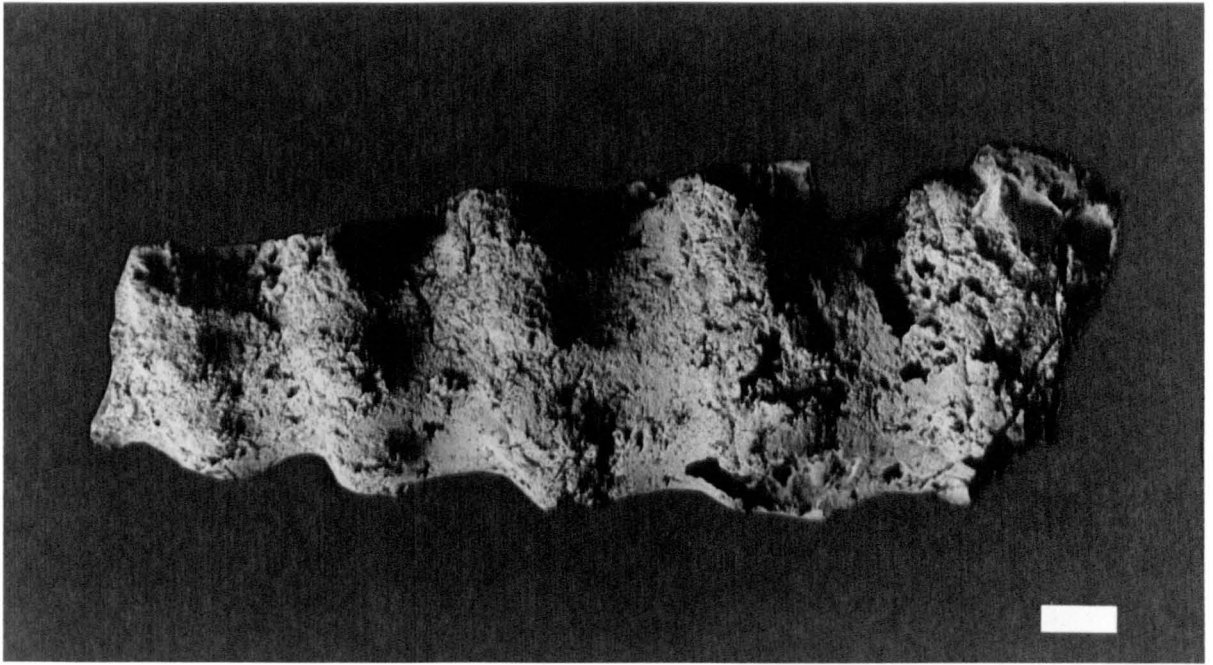


Figure 2.4a *Eunerinea vogtiana* (de Mortillet). External morphology. BM(NH) GG21885. Upper Hauterivian, Silicified Locality, Portugal.

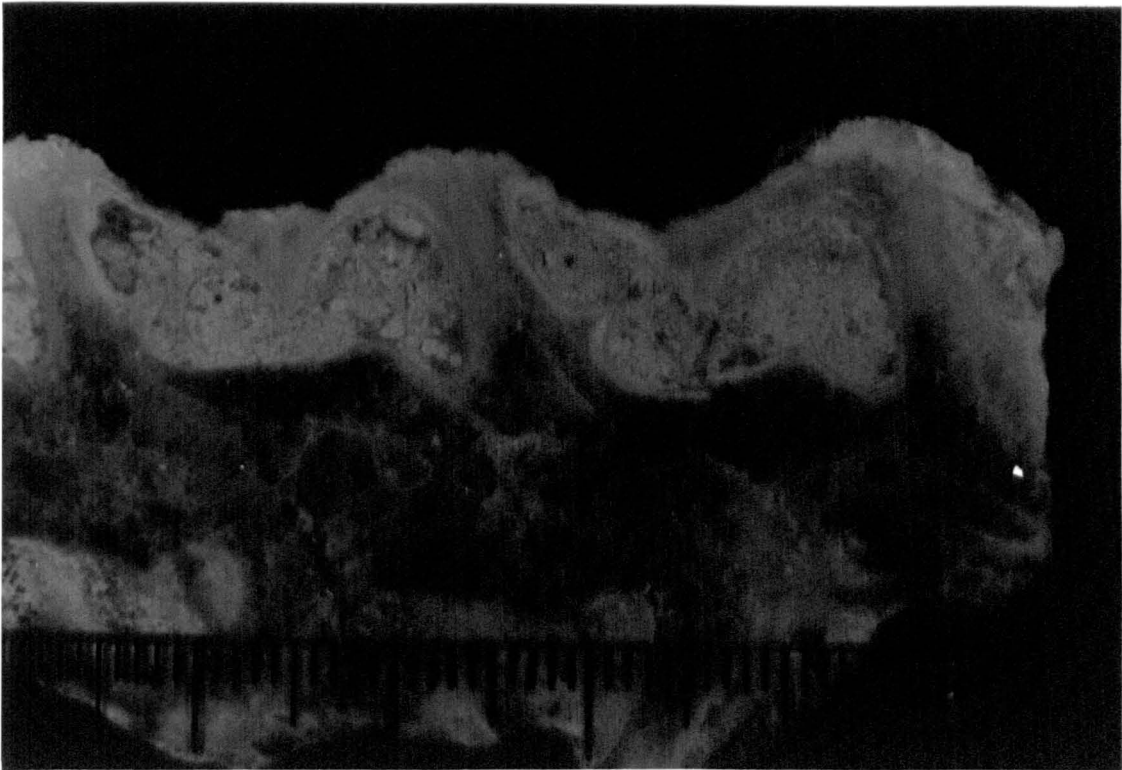


Figure 2.4b Internal morphology. BM(NH) GG21874. Upper Barremian, Calissane Chateau, France.

## Occurrence

*E. vogtiana* has been reported from France (Cossmann, 1907 and 1916a and b), Pakistan and Tunisia (Rossi Ronchetti, 1965). During the present study, it was collected in southern France and Portugal (locality numbers 7, 45).

## Stratigraphic Range

This species occurs from the Upper Hauterivian to Aptian.

### 2.8.3 Discussion of *E. archimedi* and *E. vogtiana*

There has been some confusion between the two species *E. archimedi* and *E. vogtiana*. Cossmann (1907, plate 3, figure 2) figures an *E. archimedi* specimen, which is captioned as *E. vogtiana* and is grouped together with figures of *E. vogtiana* specimens. The two species have also been closely linked together by treating *archimedi* as a variety of *vogtiana* (Petkovic, 1939; Benkőné Czabaly, 1962).

However, the present study has shown that a number of significant and consistent differences separate *E. vogtiana* and *E. archimedi* with no evidence for the existence of intermediate forms linking the two. The author considers that two quite distinct species exist (see also Rossi Ronchetti, 1965).

*E. vogtiana* has a more conical form, with a larger apical angle than *E. archimedi*. *E. vogtiana* shows greater whorl concavity, has larger and more pronounced sutural ramps with much coarser tubercular ornament. Conversely, *E. archimedi* shows a lower degree of whorl concavity together with smaller and less salient sutural ramps which bear only gently crenulated ornament. In addition, *E. archimedi* has higher whorls, with a relatively long whorl cross-section which is reflected in both the high sutural angle and the relatively high h/w ratio.

Internally, the species appear extremely similar; both have thick, non-umbilicate columellas, and the 1,1,1,0 arrangement of strong simple folds typical of the genus. Only extremely minor differences in fold shape and pattern can be observed. The columella fold in *E. archimedi* appears to be lower (ie more adapically placed) in the whorl cross-section than that in *E. vogtiana* ; also the labral fold in *E. archimedi* is slightly larger with a wider base. However, these differences are extremely subtle; the major distinguishing features are external and thus depend on reasonably good preservation.

The two species show similar stratigraphic ranges, from Hauterivian to Upper Barremian/Aptian (although *E.archimedi* has been reported from the Albian (Benkőné Czabalay, 1962)), and both are typical of urgonian-type facies. In the present study *E. archimedi* has been found to be much rarer than *E. vogtiana*.

#### 2.8.4 *EUNERINEA GIGANTEA* d'Hombres-Firmas,1838

(Figures 2.5a, b, c)

- \*1838 *Nerinea gigantea* d'Hombres-Firmas, p 207, plate 5, figures 1 and 2.
- 1843 *Nerinea gigantea* d'Hombres-Firmas; d'Orbigny, p 77, 78, plate 158, figures 1 and 2.
- 1907 *Nerinea gigantea* d'Hombres-Firmas; Cossmann, p 9 - 10, plate 1, figures 1 to 5.

##### Diagnosis

Elongate conical shell with moderately low whorls, reflected by the relatively low sutural angle. The shape and positioning of the three folds (1,1,1,0) are very characteristic of the species (see figures 5b and c).

### Material

BM(NH) GG 21897 - 21900

Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris B14763,

B14764

Étallon Collection, Department des Sciences de la Terre, Université Claude Bernard,

Lyon E14.18

### Horizons and Localities

Upper Barremian, Orgon, S of France.

### Description

Concave whorl profile, and very wide bulging rounded sutural ramps which are symmetrical about the slit-band. Ramps show relatively light crenulated ornament rather than discrete tubercles. The columella is solid and wide, occupying between 1/4 and 1/3 of the total whorl width. Distinctive quadratic whorl cross-section which is almost equidimensional.

### Measurements

Apical angle: 25° (N = 1)

Sutural angle: 102° (range 101° - 103°, N = 3)

h/w ratio: 0.45 (range 0.39 - 0.48, N = 3)

Whorl concavity index: 0.86 (range 0.85 - 0.86, N = 3)

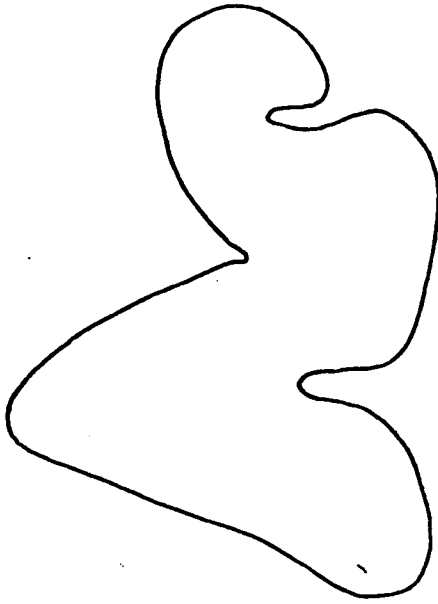


Figure 2.5c *Eunerinea gigantea* (d'Hombre-Firmas). Fold pattern in single whorl section. BM(NH) GG21899. Upper Barremian, Beau Regarde, France. Actual whorl height = 25 mm.

### Occurrence

*E. gigantea* has been reported from France (d'Orbigny, 1843; Cossmann, 1907), Spain (Coquand, 1865), Tunisia (Pervinquiere, 1912) and Algeria (Coquand, 1862). During the present study, it was positively identified from only one locality in S France, near Orgon (locality 18).

### Stratigraphic Range

This species appears to be restricted to Upper Barremian (Cossmann, 1907; own results) and Lower Aptian (Coquand, 1865) strata.

### Discussion

*E. gigantea* conforms well to the generic diagnosis, but a number of features serve to distinguish it clearly from other species in the group. These include overall shell shape, sutural ramp morphology, whorl cross-section shape and detailed fold pattern. As might be inferred from the name, *E. gigantea* specimens are often of a large size (up to about 250 mm in length, 85 mm in width) although Cossmann (1907, plate 1, figures 3 - 5) figures some "jeunes individus".



Figure 2.5a *Eunerinea gigantea* (d'Hombres-Firmas). External morphology. Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris B14763. "Urgonian", Orgon, France.

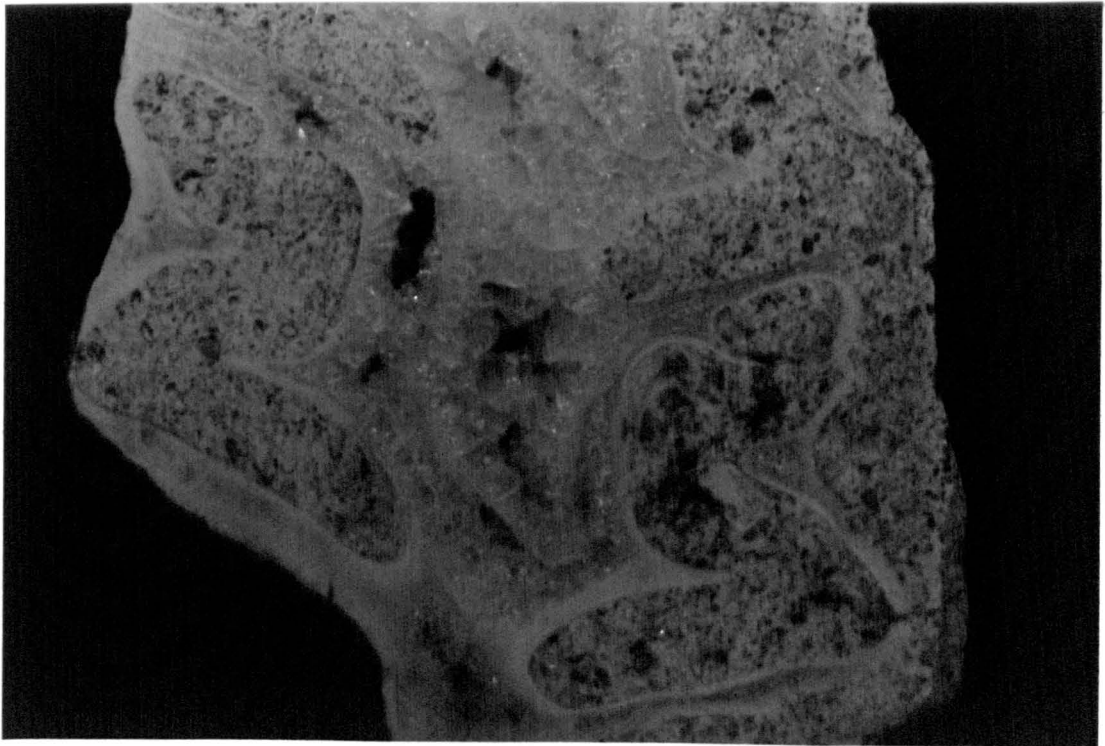


Figure 2.5b Internal morphology. Institut de Paléontologie, Muséum National d'Histoire Naturelle, Paris B14764. "Urgonian", Orgon, France.



Although the fold pattern of *E. gigantea* has not been figured in detail previously, the present study has found that the fold structure of this species is distinctive and different from that shown by other species in the genus, while still conforming to the generic pattern of 1,1,1,0.

Petkovic (1939, p74) reports "*Nerinea gigantea* d'Hombres-Firmas" (apparently a misprint of *Nerinea*, as it is later cited as *Nerinea gigantea*) from Upper Barremian strata near Belgrade, Yugoslavia. However, the drawing given (figure 12) of this species shows a specimen with a wide umbilicus, abapical carinae and a whorl cross-section much more typical of *Pchelinsevia* (see section 2.17) than of *Eunerinea*. It is therefore considered highly unlikely that this specimen belongs to *E. gigantea*, in fact, Lysenko and Aliyev (1987) have erected the species *Pchelinsevia petcovichi*, which they synonymise with Petkovic's reported "*N. gigantea*".

The limited number of reports of this species, and the fact that it has been positively identified by the present author in only one locality indicates that *E. gigantea* was relatively rare, with a rather restricted stratigraphical range.

### 2.8.5 *EUNERINEA CHLORIS* (Coquand), 1856

(Figures 2.6a,b,c)

\*1865 *Nerinea Chloris* Coquand, p 257, plate 21, figure 1.

1887 *Nerinea Chloris* Co; Mallada, p 41, plate 20, figure 1.

#### Diagnosis

Shell slenderly conical during early ontogeny, becoming markedly cylindrical in more mature specimens reflecting an extremely low expansion rate. Whorls moderately high with a concave profile and prominent rounded sutural ramps.

### Material

BM(NH) 21254, GG21936 - GG21941, GG21992 - GG21995, plus material examined and photographed insitu (locality 52).

### Horizon and Locality

Lower Albian, Comillas Coastal Section, N Spain. Albian, Santander, N Spain.



Figure 2.6a *Eunerinea chloris* (Coquand).

BM(NH) 21254. Albian, Santander, Spain.

### Description

Moderately wide solid columella. Quadratic whorl cross-section with the typical generic fold pattern 1,1,1,0. The overall morphology of this species gave rise to extremely long shells which are rather narrow when compared to other members of the genus, for example a length of 320 mm with a maximum width of 35 mm. Individual shells could reach exceptional lengths - 600 mm (BM(NH) 21254).

### Measurements

Apical Angle: 16° (range 14° - 18°, N = 5)

Sutural Angle: 109° (range 103° - 114°, N = 19)

h/w ratio: 0.58 (range 0.53 - 0.66, N = 14)

Whorl concavity index: 0.78 (range 0.73 - 0.87, N = 4)

### Occurrence

This species has been recorded from Barranco Malo, Aragon, northern Spain (Coquand, 1865) and from Santander, northern Spain (locality 52 see appendix 1). Shells which appear to be very similar to this species have been observed in Portugal (locality 51), but preservation is too poor to allow a positive identification to be made.

### Stratigraphic Range

Upper Aptian (Coquand, 1865) to at least Lower Albian (locality 52); possibly to Upper Albian (see above, locality 51).

### Discussion

Calzada (1986) discusses *Nerinea zumoffeni* Delpey in relation to *E. chloris* and concludes that the two may be synonyms (with priority for *E. chloris*). However *N. zumoffeni* has rather angular narrow sutural ramps, short thin folds and a high sutural angle. These features appear to distinguish the two species quite clearly.

*N. espaillaciana* d'Orbigny (1843, p 99 - 101, plate 164, figure 2) appears to be very similar to *E. chloris*, particularly in respect of the very cylindrical shell shape, the degree of which is unusual in the genus. D'Orbigny's figure of *N. espaillaciana* shows less salient sutural ramps than those figured by Coquand in *E. chloris* (1865, Plate 21, figure 1). However, although distinct, the two species would appear to be at least closely related.

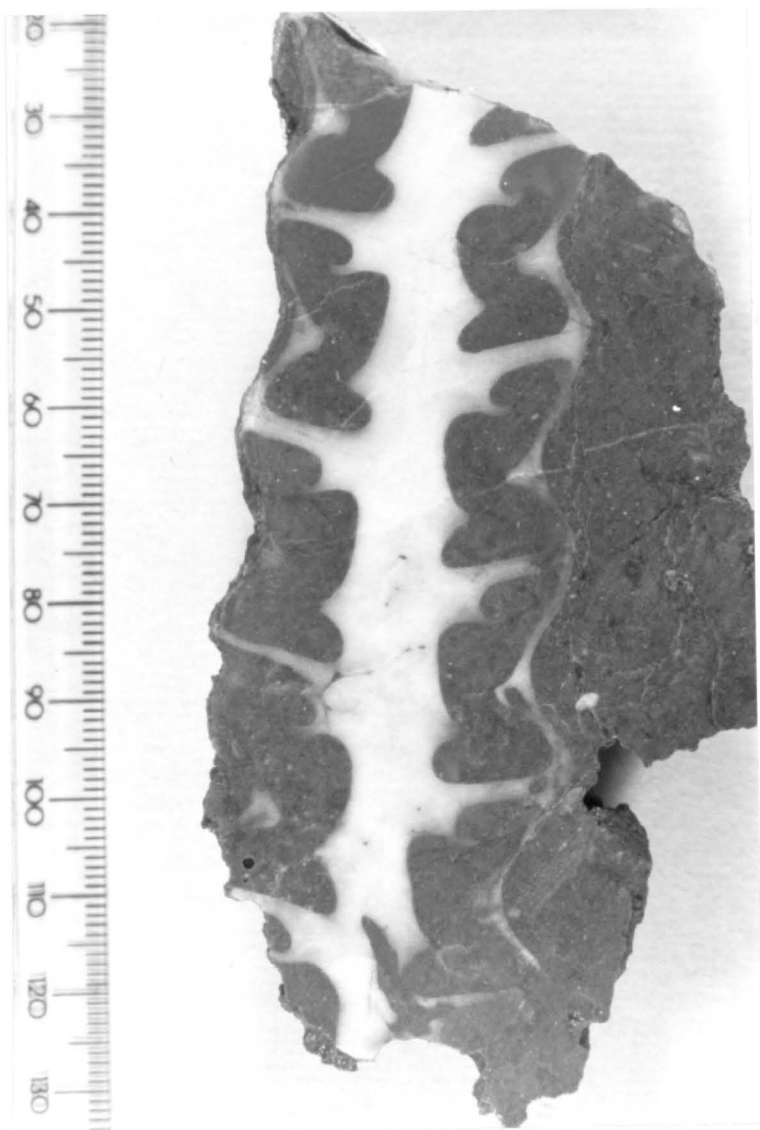


Figure 2.6b *Eunerinea chloris* (Coquand).  
Internal morphology.  
BM(NH) GG21994.  
Lower Albian,  
Comillas, Spain



Figure 2.6c Fold  
pattern in single whorl  
section. Same  
specimen as in 2.6b.  
Actual whorl height =  
20 mm

## 2.8.6 *EUNERINEA GUINCHOENSIS* (Choffat), 1886

(Figure 2.7a,b,c,d)

v\*1886 *Nerinea Guinchoensis* Choffat, p 14, plate 3, figures 15 and 16.

### Diagnosis

Thin shell, slender tapering conical shape. Pronounced narrow sutural ramp, symmetrical about the suture, bearing small-scale tubercular ornament. Moderately thin solid columella. Labral and columella folds not strongly salient.



Figure 2.7c

*Eunerinea*  
*guinchoensis*

(Choffat). Internal  
morphology.

BM(NH) GG21984.

Upper Valanginian,

Aldeia de Juzo,

Portugal.

### Material

BM(NH) GG21984 - GG21989 and (as *E. ? guinchoensis*) GG21990 - GG21991

Geological Institute Collection, Lisbon 1050 (2 specimens both figured by Choffat, 1886, plate 3, figures 15 and 16), 1051, 1053

### Horizon and Locality

Upper Valanginian, Aldeia de Juzo, Sintra Area, Portugal. As *E. ? guinchoensis* from Valanginian strata, Pointe Sublime, Verdon Gorge, S of France.

### Description

Moderately concave whorls. Long canal terminating aperture abapically. Whorl cross-section is rectangular and shows three internal folds (1,1,1,0).

### Measurements

Apical angle:  $14^{\circ}$  (range  $13^{\circ}$  -  $14^{\circ}$ ,  $N = 3$ )

Sutural angle:  $109^{\circ}$  (range  $108^{\circ}$  -  $110^{\circ}$ ,  $N = 2$ )

h/w ratio: 0.60 (range 0.55 - 0.64,  $N = 2$ )

Whorl concavity index: 0.78 (range 0.72 - 0.82,  $N = 3$ )

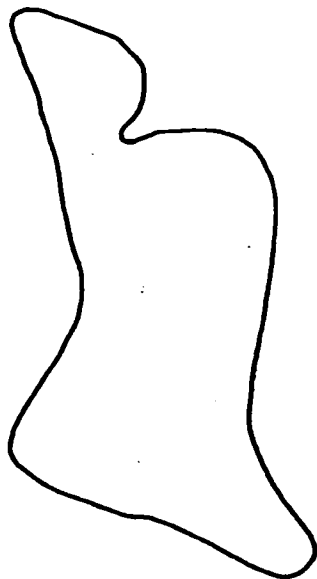


Figure 2.7d Fold pattern in single whorl section. Same specimen as in figure 2.7c. Actual whorl height = 14 mm.



Figure 2.7a *Eunerinea guinchoensis* (Choffat). External morphology. Geological Institute Collection, Lisbon 1050. No details recorded with specimen.



Figure 2.7b Internal morphology. Same registration details as in figure 2.7a.

### Occurrence

Recorded from Portugal (Choffat, 1886), also observed and collected from locality 67 (see appendix 1) in Portugal and, as *E. ? guinchoensis*, from locality 31, within the Verdon Gorge in SE France.

### Stratigraphic Range

Choffat recorded this species from the Valanginian and Lower Hauterivian. In the current study it has been recorded only from Upper Valanginian strata (Rey, 1979).

### Discussion

This species appears to be similar to *E. archimedi*, although it differs from the latter by possessing a slender columella, a narrower sutural ramp bearing more well-defined ornamentation and a distinctly weaker labral fold. The relative stratigraphic ranges of the two species, with *E. guinchoensis* extending to the Lower Hauterivian, and *E. archimedi* appearing in the Upper Hauterivian, and their morphological similarities indicate that further investigation of Hauterivian strata may reveal a phylogenetic connection between them.



## 2.9 EUNERINEA PARAMETER ANALYSIS

The four quantitative parameters given in the *Eunerinea* species descriptions are analysed graphically in histograms 2.1 to 2.4, and in graph 2.1. The raw data for these plots are given in Appendix 2. The number of measurements that are available are rather small, so the conclusions can only be drawn in general terms. However, some results are extremely interesting in respect of the previous taxonomic discussions.

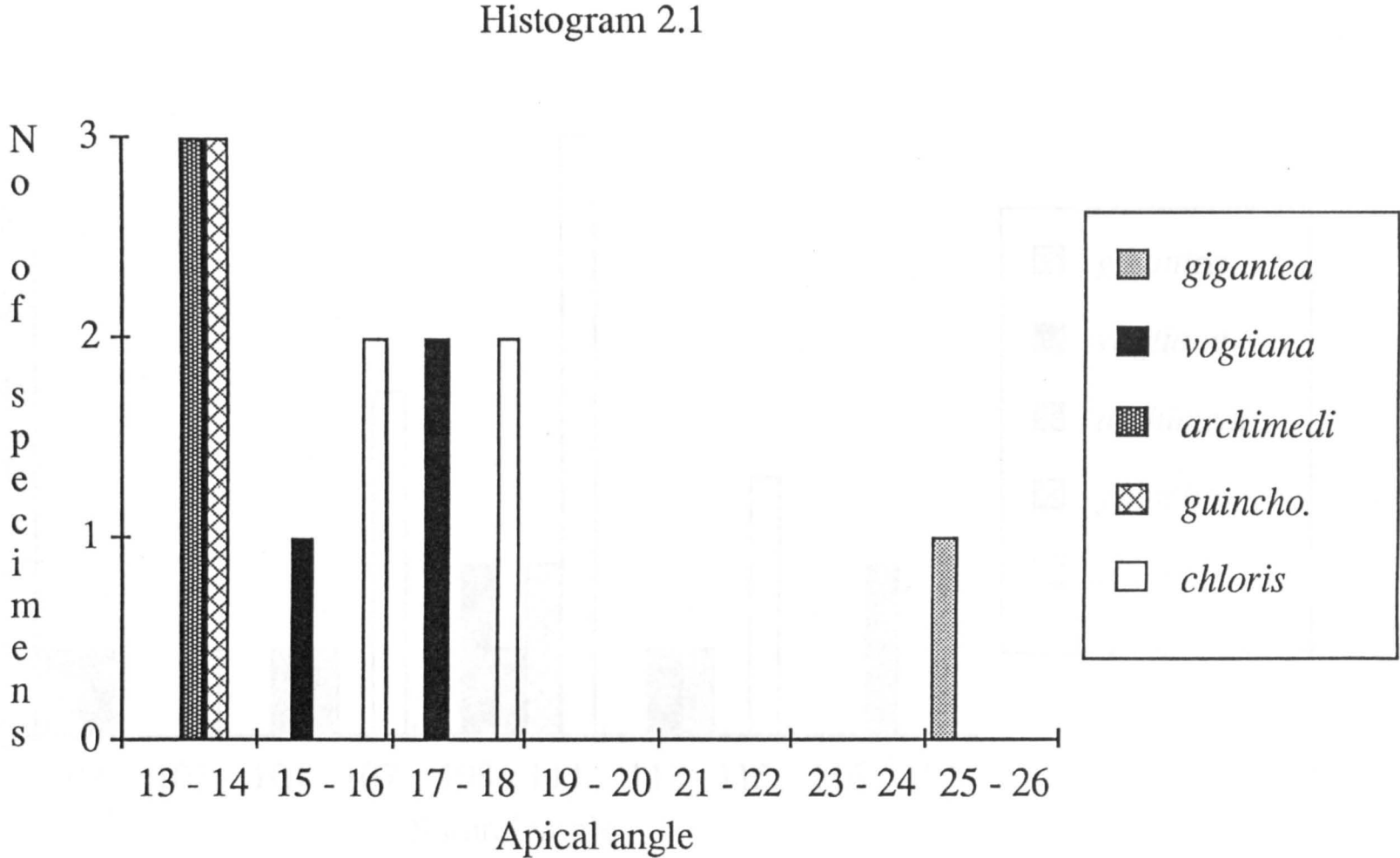
The histograms show that *E. gigantea* is distinct from the other *Eunerinea* species considered, with values at extreme ends of the scale in all cases. It shows, compared to the other species, a high apical angle and whorl concavity index and a low sutural angle and h/w ratio. In graph 2.1, of whorl concavity against h/w ratio, *E. gigantea* is clearly separated from the other species.

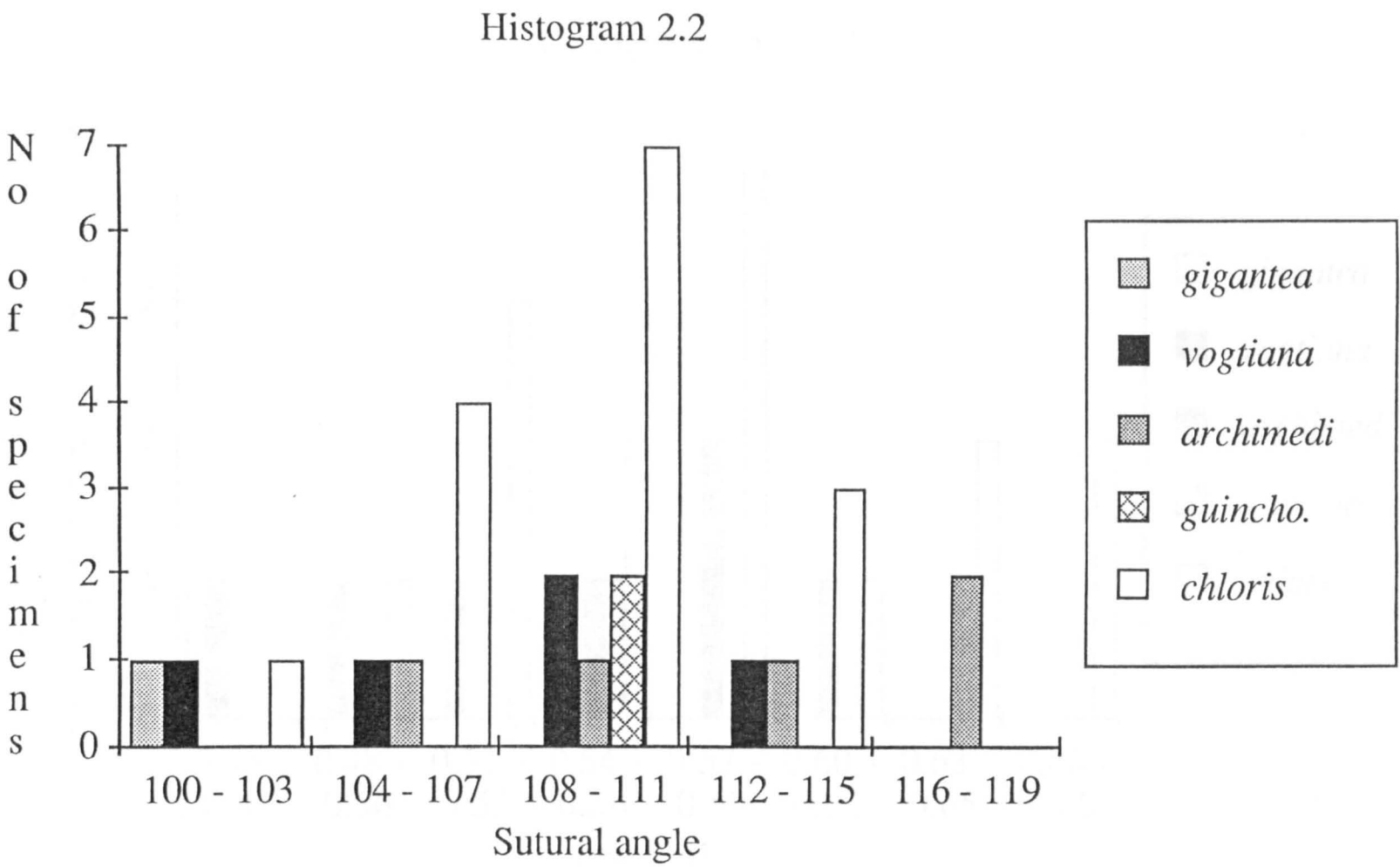
*E. guinchoensis* demonstrates in all four parameters values and ranges similar to those of *E. archimedi*, which supports the suggestion of a close phylogenetic link between the two (Section 2.8.6). In the graphical plot (graph 2.1), *E. guinchoensis* lies broadly within the area covered by *E. archimedi* values.

*E. chloris* shows parameter values that cover the whole range present within the species examined.

*E. vogtiana* and *E. archimedi* are well separated in h/w ratio and apical angle. *E. archimedi* shows a relatively low apical angle and high h/w ratio, reflecting a higher-whorled more elongate shape. In whorl concavity index there is some overlap, but *E. vogtiana* shows a trend towards lower values, indicating a greater degree of concavity. Sutural angle values show a wide range in both species and considerable overlap occurs. However, in the graphical plot of whorl concavity against h/w ratio (graph 2.1), the two species occupy quite distinct plot areas. These results support the separation of *E. vogtiana* and *E. archimedi* as separate species (discussed in Section 2.8.3).

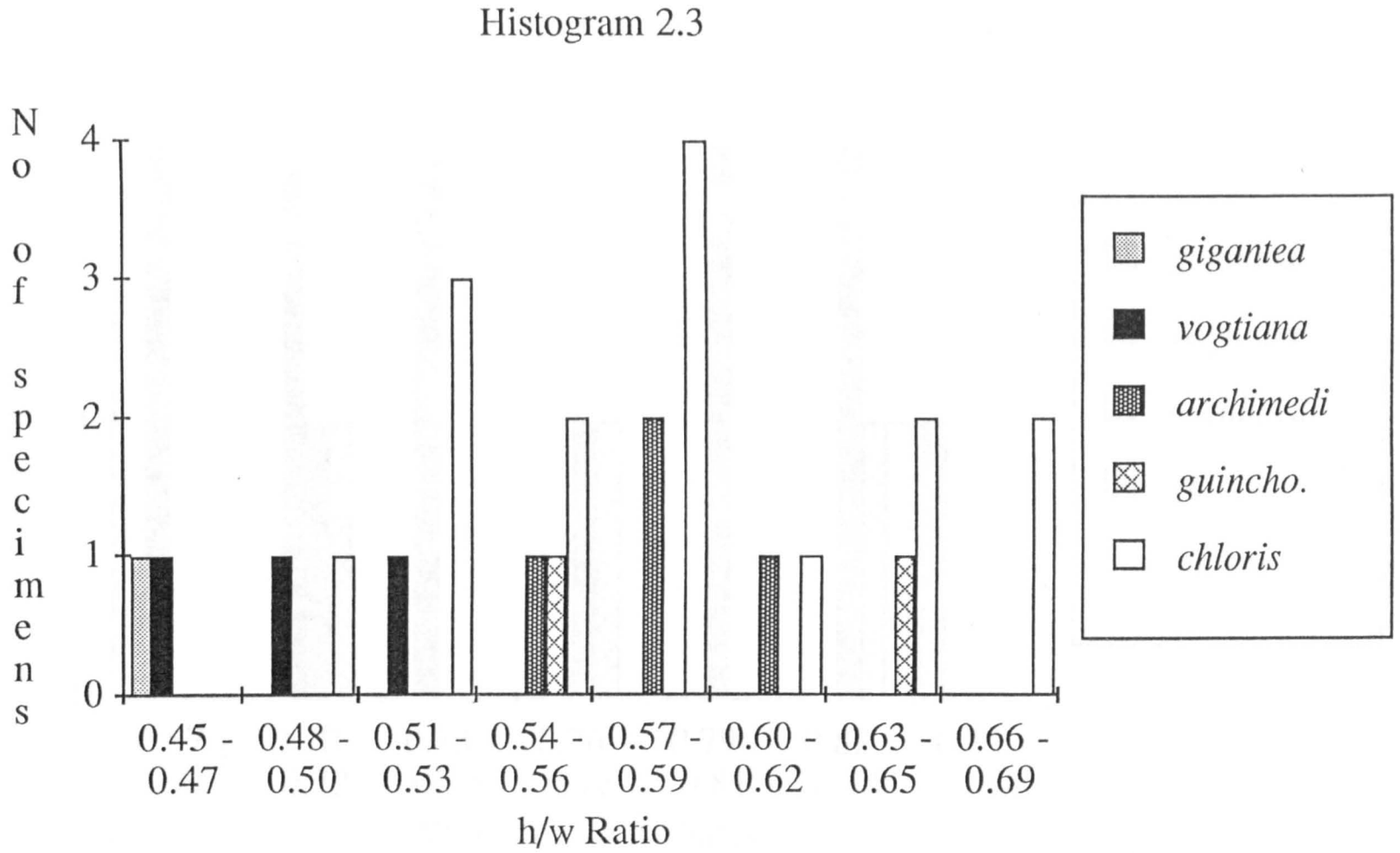
Histogram 2.1 Apical angle measurements in *Eumerinea* species.



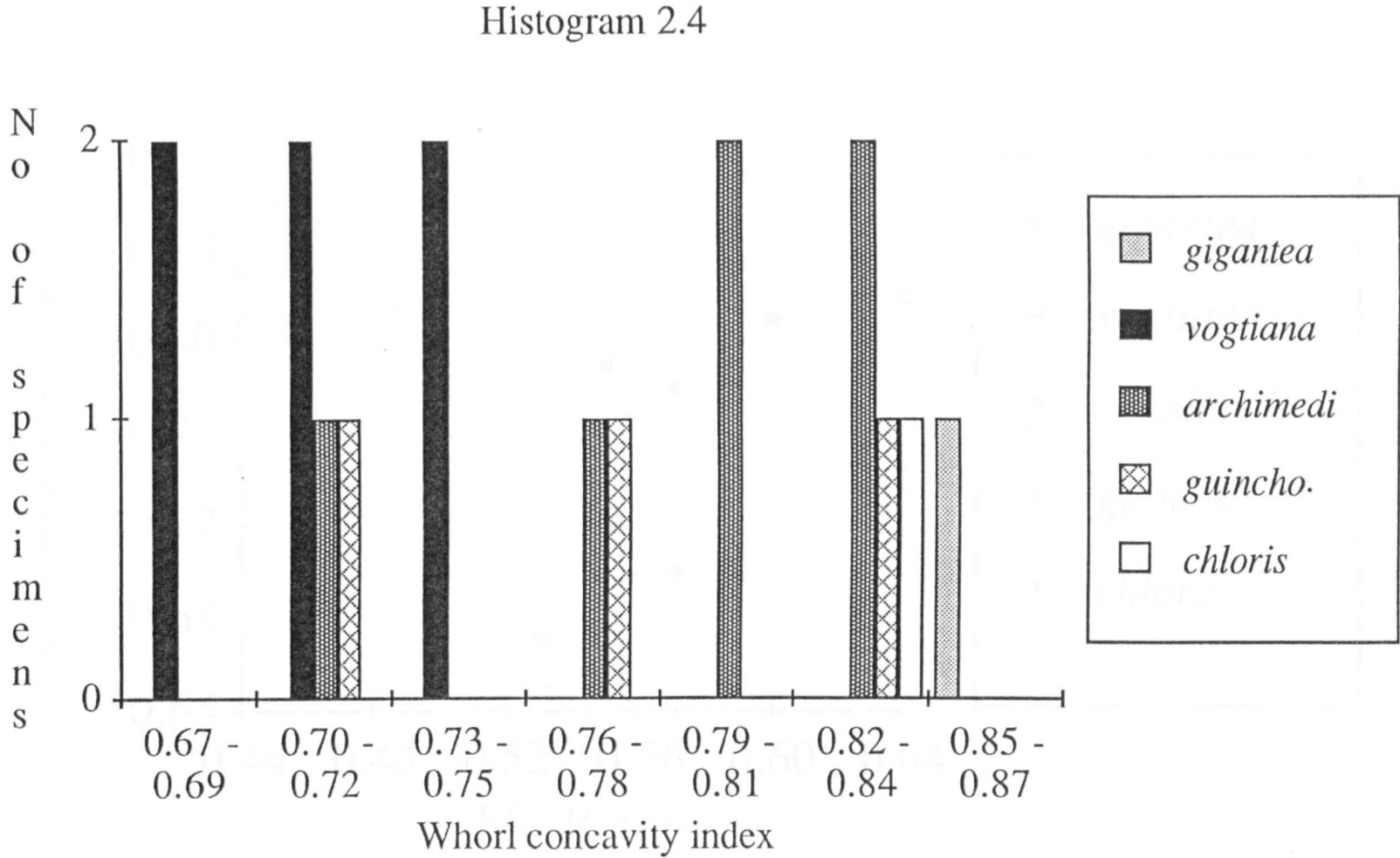


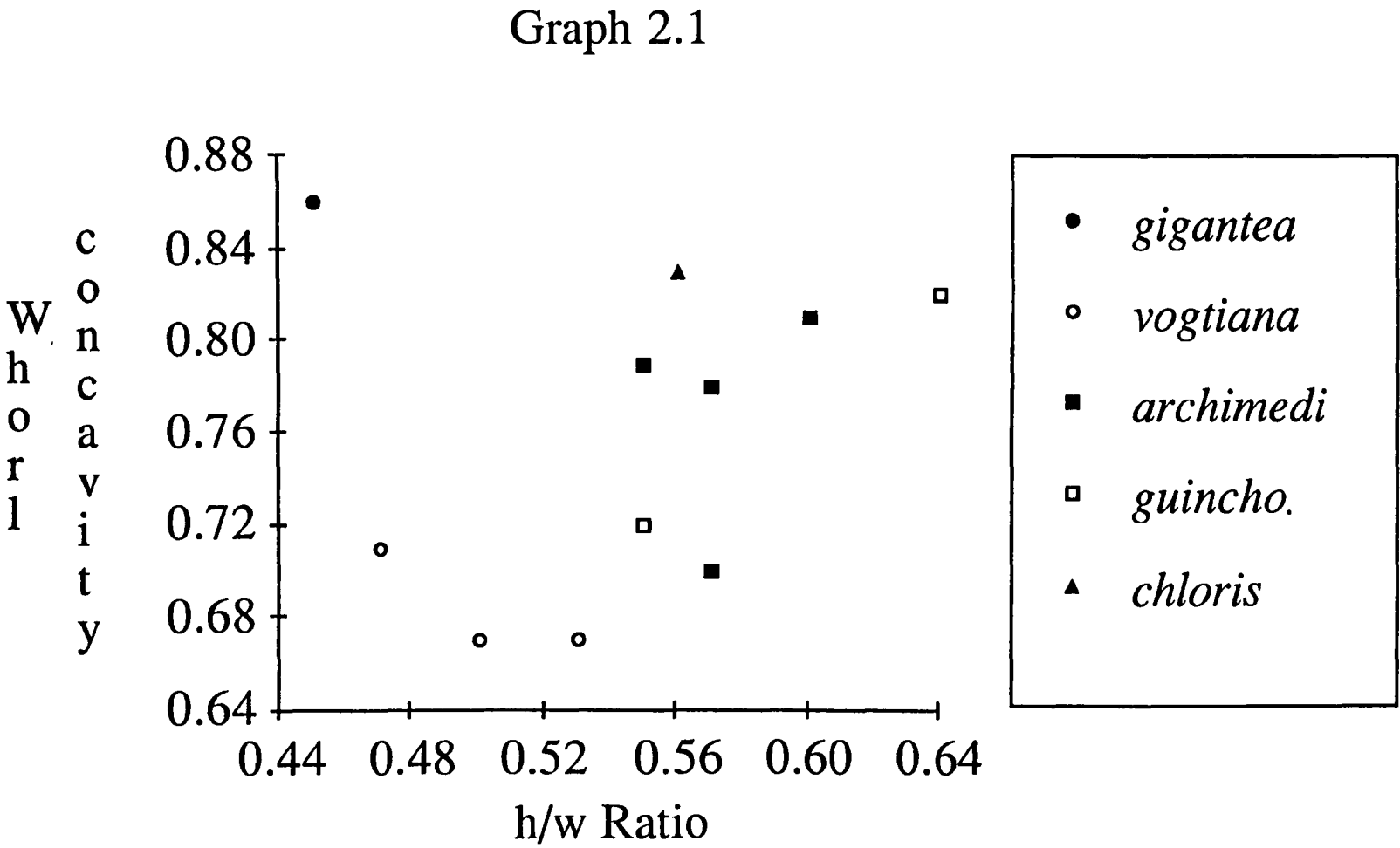
Histogram 2.2 Sutural angle measurements in *Eumerinea* species.

Histogram 2.3 h/w Ratio measurements in *Eumerinea* species.



Histogram 2.4 Whorl concavity index measurements in *Eumerinea* species.





Graph 2.1 Scattergraph of h/w ratio against whorl concavity index for *Eunerinea* species.

## 2.10 Genus *DIOZOPTYXIS* Cossmann, 1896

Type species. *Diozoptyxis monilifera* Cossmann, 1896 [not *Nerinea monilifera* D'Orbigny, 1843]

### Discussion

*Diozoptyxis* was erected as a subgenus of *Nerinea* sensu stricto by Cossmann (1896) with the type species *Nerinea monilifera* d'Orbigny. The essential features of this subgenus given by Cossmann included:-

"a conical shell with numerous narrow, stepped whorls, each ornamented by rows of rounded tubercles, and perforated by a narrow umbilicus. Aperture quadrangular, subcanaliculate at the base with a salient labral fold and two columella ones"<sup>1</sup>.

As well as the type species, Cossmann included *Nerinea pailleteana* d'Orbigny and *N. marrotiana* d'Orbigny within the subgenus *Diozoptyxis*, although it is now clear that neither of these two species conform to Cossmann's diagnosis. Cossmann (1907) later included *Nerinea renauxiana* d'Orbigny and *N. coquandiana* d'Orbigny in this subgenus.

### 2.10.1 The Type Species of *Diozoptyxis*

Cossmann (1896) designated *Nerinea monilifera* d'Orbigny as the type species of *Diozoptyxis*. However, Cossmann's diagnosis, which was based on a specimen from

---

<sup>1</sup>"Forme ..... conique ..... tours nombreux, très étroits, en gradins, ..... ornés de deux rangs de tubercules arrondis ..... perforée au centre d'un étroit entonnoir ombilical. Overture quadrangulaire .....subcanaliculée à la base; un pli spiral très saillant à l'intérieur du labre ..... deux plis columellaires, pas de pli parietal." Cossmann, 1896, p 31.

Le Mans in the Nantes Museum Collection, differed in a number of respects from d'Orbigny's (1843) description and figures of *N. monilifera*. It appears that externally, the descriptions and figures are very similar, but that the internal structure specified is different. D'Orbigny describes one weak parietal fold, whereas Cossmann states that there are two columella folds and a strong labral one. In addition, d'Orbigny indicates that the shell is "non ombiliquée" (1843, p 95), whereas Cossmann notes an "étroit entonnoir ombilical" (1896, page 31). It seems highly unlikely that the specimen described by Cossmann belongs to d'Orbigny's species.

The author has been unable to locate any specimens described as *N. monilifera* in the d'Orbigny Collection housed at the Muséum d'Histoire Naturelle in Paris, and is currently in correspondence both with this museum and Nantes Museum in an attempt to locate both d'Orbigny's and Cossmann's specimens. However, Cossmann's description of "*N. monilifera*" is at such variance with d'Orbigny's description of the species that it seems probable that "*N. monilifera*" sensu Cossmann is a different species. ICZN (1985) Article 70c applies in this case, Note (i) of which states:-

"..... the new nominal species has the same species-group name as was misapplied but it is combined with the new generic or subgeneric name"

ICZN, 1985, p 139

Hence "*Nerinea monilifera*" sensu Cossmann becomes a new species *Diozoptyx monilifera*, the holotype of which (by original designation - ICZN Article 73a (i)) is from Le Mans, France, and should be housed in the Nantes Museum Collection.

Delpey (1939) placed some specimens which she identified as "*Campanile (Diozoptyx) moniliferum* d'Orbigny" in the Campanilidae:- "Cette coquille qui est l'un des premiers *Campanile* connus" (p 210) (This shell which is one of the first known campanilids). However, her description and drawn figures do not appear to resemble either d'Orbigny's or Cossmann's concepts of *N. monilifera*, and the author considers it



highly unlikely that the specimens involved belonged either to *Nerinea monilifera* d'Orbigny or *Diozoptyx monilifera* Cossmann.

However, there remains some doubt as to whether *N. monilifera* d'Orbigny is a nerineid or a campanilid. D'Orbigny's description and figures do not allow any firm conclusions to be drawn. The specimens currently available to the author (BM(NH) 81491 and 32358, both from the Cenomanian of Le Mans) do not have any internal structure preserved, and it is therefore difficult to distinguish whether they belong to *N. monilifera* or *D. monilifera*. In any case the specimens are not sufficiently well-preserved externally to show any of the features which might indicate either nerineid or campanilid affinities (eg growth lines, selenizone, protoconch etc). The resolution of this problem must therefore be postponed until better preserved material can be examined.

If *N. monilifera* is a campanilid, this would be one of the earliest species of this group<sup>1</sup>, which was regarded by Cossmann (1906) as appearing at the end of the Cretaceous, although he does mention some specimens from the Barremian and Turonian which resemble campanilids. Delpey (1941) mentions five campanilid species, including *N. monilifera* d'Orbigny, from Cenomanian strata which she considers to be the very earliest representatives of *Campanile*, and Abbass (1973) described ?*Campanile cenomanica* Abbass from the ?Cenomanian of Dorset.

*D. monilifera* almost certainly belongs to the Nerineidae, and therefore *Diozoptyx* is a nerineid genus. The strong labral fold mentioned by Cossmann is atypical of the Campanilidae; the author has not encountered any campanilid species which has labral

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<sup>1</sup>*N. monilifera* is recorded by d'Orbigny as occurring in "les couches les plus inférieures des craies chloritès ..... dans la seconde zone de Rudistes avec la *Caprina adversa*" (d'Orbigny, 1843, p96) which appears to indicate a Cenomanian age (Delpey, 1939; Skelton, pers comm).

folds, although Delpey (1941) records "*Nerinea-Campanile Ciryi* Delpey" as having a weak labral fold.

The confusion concerning *Diozoptyx*, *N. monilifera* and *D. monilifera* has led to an unfortunate association of *Diozoptyx* with *Campanile* (Delpey, 1939 and 1941; Cox, 1954; Houbrick, 1981; Lysenko and Aliyev, 1987).

The following points arise from the above discussion:-

- 1 *N. monilifera* d'Orbigny and *D. monilifera* Cossmann are distinct species.
- 2 *N. monilifera* d'Orbigny may or may not belong to the Campanilidae.
- 3 *D. monilifera* Cossmann is a nerineid and there is no reason to associate this species with the Campanilidae.
- 4 *D. monilifera* is the type species of *Diozoptyx*.
- 5 *Diozoptyx* therefore belongs to the Nerineidae

## 2.11 Genus **ADIOZOPTYXIS** Dietrich, 1914

Type species. By subsequent designation (Cox, 1954), *Nerinea polymorpha* Gemmellaro, 1865.

### Discussion

Dietrich (1914) apparently erected<sup>1</sup> a subgenus group to include species which conformed to Cossmann's diagnosis except in respect of ornamentation (Cox, 1954).

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<sup>1</sup>"Aber soll ich deswegen etwa eine "Untergattung" *Adiozoptyxis* aufstellen für die sich in der genannten *N. Polymorpha* Gemm., ferner in *N. pyriformis* Gemm. (a.a. O., t. 3, f. 1 & 2) u. a. europäische Vertreter namhaft machen ließen?" Dietrich, 1914, p 141 (But should I make a subgenus *Adiozoptyxis* in which I

The term "*Adiozoptyxis*" was mentioned in connection with *Nerinea polymorpha* Gemmellaro and *Nerinea pyriformis* Gemmellaro, and later Dietrich (1925, page 108) mentioned *Adiozoptyxis* as a new subgenus in connection with *N. polymorpha* (in this case referred to as *Phaneroptyxis polymorpha*). In the same work, a number of species were referred to as belonging to *Diozoptyxis*, following Cossmann's diagnosis of the group.

## 2.12 SUBSEQUENT REVISION OF *DIOZOPTYXIS* AND *ADIOZOPTYXIS*

The diagnosis of *Diozoptyxis* was emended by Pchelintsev (1931, cited in Pchelintsev, 1968 p 25) so as to allow umbilical width to vary from narrow to wide, whorl profile to range from flat to concave with either a smooth or tuberculate sutural ramp and specifying the presence of an intraumbilical carina. Pchelintsev (1968) incorrectly indicated *N. renauxiana* as the type species of the emended genus (ICZN, 1985, Article 69a). A number of species were mentioned in connection with this emended genus, all of which are considered by the author to belong to the Umboneidae (see below).

Cox (1954, p 12) proposed that *Adiozoptyxis* should become a genus containing both smooth and tubercular ornamented species which conformed to the diagnosis:

"Shell moderately stout, often large with broad umbilicus; whorls low, strongly concave to flat, smooth or tuberculate, with an angular adaxial projection forming a helix within the umbilicus. Details of aperture unknown. Three internal folds present (2,0,1,0 or 1,1,1,0)"

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could put *N. polymorpha* Gemm. and especially *N. pyriformis* Gemm. (and other) European forms, or should I leave them alone?

Within the emended *Adiozoptyxis*, Cox included *Nerinea pillae* Gemmellaro, *N. coquandiana*, *N. renauxiana*, *N. valdensis* Pictet and Campiche, and also apparently *N. polymorpha* and *N. pyriformis*.

### 2.13 REVISION OF *DIOZOPTYXIS* AND *ADIOZOPTYXIS*

The genera *Diozoptyxis* and *Adiozoptyxis* are in a confused state; the latter in particular has had included within it (Cox, 1954) species possessing a wide variety of shell morphologies which, although they share a number of basic features such as fold number and arrangement, the presence of an umbilicus with carina etc, show profound differences in other features which indicate that they are not closely related. In particular the combining of species showing whorl overlap (eg *N. polymorpha*, *N. pyriformis*) with those where no whorl overlap occurs (eg *N. coquandiana*, *N. valdensis*), and also the range allowed in umbilical width, overall shell shape, and whorl height all demonstrate that the present groupings in *Adiozoptyxis* (and *Diozoptyxis*) do not represent a phylogenetic unit.

There appear to be three major divisions into which the species associated with *Diozoptyxis* and *Adiozoptyxis* fall. These groups do not appear to be closely related, and should be regarded as totally separate and independent of each other. Their association together has been the unfortunate result of the non-critical application of a rather imprecise generic diagnosis. Revised generic diagnoses of the groups involved are set out below; these are considered to closely reflect the respective authors' original concept of their genus.

## 2.14 Genus *DIOZOPTYXIS* Cossmann, 1896

Type species. *Diozoptyx monilifera* Cossmann, 1896 [not *Nerinea monilifera* D'Orbigny, 1843]

### Revised Diagnosis

Conical shell, coeloconoid to cyrtconoid in shape, reaching small to moderate size (up to 70 mm in length). Numerous low whorls; whorl profile strongly to weakly concave (degree of concavity may vary through ontogeny) with pronounced sutural ramp developed bearing medium to fine scale tubercular ornament. Very fine corded helical striae may occur on the external surface between the sutural ramps. There is no tendency for later whorls to envelop earlier ones. Narrow umbilicus which may not be visible externally. Quadrangular whorl cross-section with three strong simple folds (1,1,1,0 or 2,0,1,0 depending on interpretation of position of a fold in the parieto-columella corner).

Essential distinguishing features: low whorls, narrow umbilicus, no tendency for whorls to overlap.

Species: *D monilifera* Cossmann, *Nerinea cochleaeformis* Conrad (= *D. cochleaeformis* (Conrad), ?*Nerinea fleuriau* d'Orbigny (sensu Delpey, 1939) (= ?*D. fleuriau* (d'Orbigny)).

Stratigraphic range: Albian - Turonian

### Discussion

This group is basically the genus *Diozoptyx* as first set up by Cossmann (1896) with an emended diagnosis. This genus shows restricted diversity; many of the different "species" which would have been included in this group apparently belong to one single species (*N. cochleaeformis*) which is rather variable (see Chapter 3).

## 2.15 Genus *ADIOZOPTYXIS* Dietrich, 1914

Type species. By subsequent designation (Cox, 1954), *Nerinea polymorpha* Gemmellaro, 1865.

### Revised Diagnosis

Rounded, blunted conical shells. Whorl walls thick; whorl profile flat or convex, slight bulging in region of suture may be present, restricted to abapical side of the suture. Shell surface smooth or with light large scale crenulation. Moderate to wide umbilicus into which rounded abapical carinae project. Whorl cross-section shows very thickened whorl walls with reduced whorl space which is triangular to oval in shape. Later whorls overlap earlier ones covering about half the total height of the preceding whorl. Three rounded simple folds present (1,1,1,0) which do not project far into the whorl cavity.

Essential distinguishing features: overlapping whorls, shell shape, fold shape and degree of fold prominence.

Species: *N. polymorpha* Gemmellaro (= *A. polymorpha* (Gemmellaro)), *N. pyriformis* Gemmellaro (= *A. pyriformis* (Gemmellaro))

Stratigraphic range: Upper Jurassic

### Discussion

It is possible that this group is allied to *Phaneroptyxis* and thus has some affinities with the Itieriidae. Dietrich (1925, p 108) listed the species *polymorpha* within *Phaneroptyxis*, and mentions *Adiozoptyxis* as a new subgenus in the discussion of this species. *Adiozoptyxis* differs from *Phaneroptyxis* in the degree of whorl overlap and the elongation of whorl shape, both of which are considerably greater in *Phaneroptyxis*; Cossmann (1896, p 22) specified and figured a last whorl which was equal to at least

half the total shell length. In other respects the two groups are similar and *Adiozoptyx* may be an intermediate form linking Nerineidae genera with the Itieriidae, although much more precise stratigraphic information is required before this possibility can be supported. The overall shape of *Adiozoptyx* and the degree of whorl overlap are not considered to indicate that a placing within the Itieriidae would be appropriate. The genus is thought to belong within the Nerineidae.

## 2.16 Sub-Family UMBONEINAE Lysenko and Aliyev, 1987

[name emended and corrected herein ex Umboneidae Lysenko and Aliyev, 1987]

### Revised Diagnosis

Conical shells - regular or cyrtocoid, which can reach large sizes (up to 220 mm in length). Whorls moderate to high (h/w ratio typically between 0.30 - 0.50); whorl profile from strongly concave to flat. No tendency for whorl overlap to occur. If present, the sutural ramp may bear coarse tubercular ornament. Moderate to wide umbilicus into which prominent abapical carinae project. Whorl cross-section is quadratic to triangular with 3 prominent simple folds (1,1,1,0).

Essential distinguishing features: absence of whorl overlap, height of whorls, width of umbilicus (usually visible externally ).

Species: *N. toucasaiephila* Dietrich (= *Pchelinsevia. toucasaiephila* (Dietrich)), *N. coquandiana* d'Orbigny (= *P. coquandiana* (d'Orbigny)) *N. valdensis*. Pictet and Campiche (= *P. valdensis*. (Pictet and Campiche)).

Stratigraphic range: Valanginian - Aptian

## Discussion

Pchelintsev (1968) set up a "family Diozoptyxidae" consisting of the genera *Umbonea* Pchelintsev, *Neoptyxis* Pchelintsev and *Diozoptyxis* Cossmann emend Pchelintsev.

Lysenko and Aliyev (1987) revised Pchelintsev's work in respect of ICZN rules and their own research; they made the following proposals:-

- 1 A new "family Umboneidae" Lysenko and Aliyev containing the genera *Umbonea*, *Pchelinsevia* Lysenko and Aliyev and *Affiniptyxis* Lysenko and Aliyev.
- 2 *Diozoptyxis* is a "younger" synonym of *Campanile*.

The reasons for rejecting the second proposal are outlined above.

The subfamily Umboneinae, although rather poorly characterised by Lysenko and Aliyev (1987), appears to represent a true phylogenetic unit. The present consideration of the group as a subfamily rather than a family is discussed on page 36. The three genera appear to be well-defined; they are separated on the basis of "spiral folding and the form of the umbilicus" (Lysenko and Aliyev, 1987, p 128), together with the morphology of the intraumbilical carinae.

## Incertae subfamiliae

### Genus *DIOZOPTYXIS* Cossmann, 1896

#### 2.17 *DIOZOPTYXIS COCHLEAEFORMIS* (Conrad), 1852

(figures 2.8, 3.1 and 3.2)

1852 *Nerinea cretacea* Conrad, p 227, plate 16, figure 85.

\*1852 *Nerinea? cochleaeformis* Conrad, p 233, plate 4, figure 29.

p.1852 *Nerinea Syriaca* Conrad, plate 5, figures 34 and 38 only.



- 1862 *Nerinea gemmifera* Coquand, p 177 - 178, plate 4, figure 4.
- (?)1867 *Nerinea Mamillae* Fraas, p 241 - 242, plate 4, figure 6.
- 1877 *Nerinea gemmifera* Coquand; Lartet plate 9, figure 8.
- 1878 *Nerinea gemmifera* Lartet; Fraas, plate 6, figure 2.
- 1884 *Nerinea pauxilla* Hamlin, p 25 - 26, plate 2, figure 4.
- p.?1890 *Nerinea Mamillae* Fraas; Blanckenhorn, plate 8, figures 5a and b only.
- (?)1900 *Nerinea cochleaeformis* Conrad; Böhm, p 205, plate 7, figures 1, 2, 2a, 9, 9a.
- .p.1906 *Nerinea cochleaeformis* Conrad; Oppenheim, plate 8, figures 1, 3, 4 and 5 not figure 2 and text figure 3.
- 1927 *Nerinea cochleaeformis* Conrad; Blanckenhorn, p 150 - 152, plate 3, figures 57 - 59.
- .1939 *Nerinea cretacea* Conrad; Delpey, p 191 - 192, plate 7, figures 2 - 6.
- .1939 *Nerinea gemmifera* Coquand; Delpey, p 193, plate 7, figures 7 - 9.
- .1939 *Nerinea gemmifera* Coquand var *subgigantea* Blanckenhorn; Delpey, p 194, plate 7, figure 10.

### Diagnosis

Variable shell shape ranging from narrowly conical isometric form to bulging conical cyrtconoid shape (figure 3.2). Moderately low whorls with markedly concave profile and pronounced rounded sutural ramps bearing medium scale knotted tubercular ornament.

### Material

BM(NH) 83694, G17262, G19451

### Horizon and Locality

?Turonian, Gazelle Hollow and Gazelle Mountain, Abeih, Lebanon

### Description

Finely knotted spiral striae present in concavity of whorl. Columella is narrowly open showing a poorly developed umbilicus. Quadratic whorl section with three folds (1,1,1,0). A heterostrophic protoconch is present (Chapter 6).

### Measurements

Apical angle: highly variable

Whorl concavity index: 1.26 (range 1.11 - 1.38, N = 31)

### Distribution

This species, under its various aliases, has been reported from the Middle East (Conrad, 1852; Lartet, 1877; Delpey, 1939), North Africa (Algeria) (Coquand, 1862) and south west France (Oppenheim, 1906).

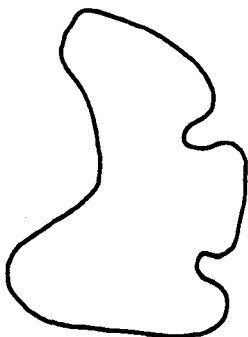


Figure 2.8 *Diozoptyx cochleaeformis* (Conrad). Fold pattern in single whorl section. BM(NH) G17262. ?Turonian, Gazelle Hollow, Lebanon.

### Stratigraphic Distribution

*D. cochleaeformis* is reported mainly from Turonian strata (Coquand, 1862; Blanckenhorn, 1927) although Delpey (1939) gives a range from the Upper Albian to Turonian.

### Discussion

The morphological range present in this species is fully analysed and discussed in Chapter 3. One of the conclusions resulting from this study is that although

considerable variation is present it is occurring within a single morpho-species. This morphological variability, which appears to be a characteristic feature of *D. cochleaeformis*, has caused considerable taxonomic confusion. The synonymy list given above shows that a number of "different" species and varieties have been erected, all apparently based on *D. cochleaeformis* specimens. The range in shape shown by this species has obviously contributed to this plethora of different names. In addition, poor species characterisation, both in terms of description and figures, in earlier works (Conrad, 1852; Fraas, 1867) has led to poor comprehension of specific characters and subsequent misinterpretation of the species group. The situation has been further obscured by the loss of many of Conrad's type specimens<sup>1</sup>. This loss is particularly unfortunate in that the type of the original species (*D. cochleaeformis*) was not available to subsequent authors, and also the types of the other two species; *N. cretacea* and *N. syriaca* (part only) thought to be synonymous with *D. cochleaeformis* were also unavailable for comparison.

Despite these problems, several authors synonymised *D. cochleaeformis* with some or all of the species given above (Böhm, 1900; Blanckenhorn, 1927; Delpy, 1939). Blanckenhorn (1927) appears to have been the first worker to synonymise *N. cretacea* with *N. cochleaeformis*. As both of these names were published in the same work (and on the same date) this places him in the position of First Reviser; the name which he chose to use for the species group, *N. cochleaeformis*, therefore becomes the valid name of the species by the Principle of First Reviser (ICZN, 1985, Article 24 a and b).

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<sup>1</sup>"I have made every reasonable effort to find the originals of Mr. T. A. Conrad's species ..... they seem, however, to have been entirely lost sight of, as inquiries of the different societies and persons having charge of collections, where they might have been deposited, have entirely failed to bring any of them to light" Whitfield, 1891, p 383.

Delpey (1939) considered that two species were present, "*N. cretacea*" (an invalid use of this term - see above), and "*N. gemmifera*"; two varieties were also associated with the latter - "*subgigantea*" Blanckenhorn and "*ghazirensis*" Delpey. The main distinction used to separate these two species was the presence of fine striae in the whorl concavity of "*N. cretacea*"<sup>1</sup> whereas these are absent in "*N. gemmifera*"<sup>2</sup>. Delpey notes, however, that this distinguishing feature may simply reflect the loss of this type of ornamentation either during ontogeny (as is seen, for example, in ?*P. schicki*, section 2.27.1) or as the result of poor preservation. The measurements and figures given show that the "*N. gemmifera*" specimens were all considerably larger, representing much later ontogeny, than the "*N. cretacea*" material. Delpey acknowledges that "*N. gemmifera*" may prove to be no more than mature specimens of "*N. cretacea*"<sup>3</sup>.

The author considers that "*N. cretacea*" and "*N. gemmifera*" are indeed the same species, and that, together with the other species names given in the synonymy list, these names are subjective junior synonyms of *D. cochleaeformis*.

### Varieties

The variation present within *D. cochleaeformis* appears to be continuous in nature. It does not therefore seem appropriate to separate the species into "varieties" as these do not reflect any natural divisions, and do not usefully contribute to the study of this species.

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<sup>1</sup>"La partie concave des tours est ornée de trois ou quatre filets granuleux" Delpey, 1939, p 192.

<sup>2</sup>"La partie concave des tours ne porte que des stries d'accroissement transversales" Delpey, 1939, p 193

<sup>3</sup>"Il est possible que cette espèce, toujours étudiée sur des échantillons érodés ou brisés, ne soit qu'une forme adulte de *N. cretacea* dont l'ornementation fine s'effacerait avec l'âge, comme cela observe chez d'autres Nérinées" Delpey, 1939, p 193.

Delpey's variety "*N. gemmifera* var. *ghazirensis*" is distinguished "par la section du tour et la disposition des plis (Delpey, 1939, p 195) (by the whorl section and the fold arrangement), in particular "un pli labial très faible" (p 194) (a very weak labral fold). Judging from Delpey's photographs (plate 7, figures 11<sup>1</sup> and 12) of this "variety" the labral fold appears to be totally absent in these specimens, which probably belong to *Diptyxis*.

### Subfamily Umboneinae Lysenko and Aliyev, 1987

#### 2.18 Genus *PCHELINSEVIA* Lysenko and Aliyev, 1987

Type species. By original designation with name correction applied herein, *N. coquandiana* d'Orbigny, 1843.

#### Comment

*Pchelinsevia*, with the invalidly cited type species *Nerinea renauxiana* d'Orbigny appears to be equivalent to Pchelintsev's invalid "*Diozoptyxis* Cossmann emend Pchelintsev". However, *N. renauxiana* has been synonymised (Douville, 1926; Delpey, 1939, and see below) with *N. coquandiana* d'Orbigny, and as the latter name has priority (as it was the first name used in the first formal synonymy proposed by Delpey (1939)) under the Principle of First Reviser (ICZN, 1985, Article 24 (a)), the type species of *Pchelinsevia* should be recorded as *N. coquandiana*.

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<sup>1</sup>In this figure, uneven preservation of shell thickness gives an apparent trace of a labral fold.

### 2.18.1 *PCHELINSEVIA TOUCASIAEPHILA* (Dietrich), 1914

(Figures 2.9a,b,c,d)

\*1914 *Nerinea (Diozoptyxis) toucasiaephila* Dietrich, p.139, text fig. 2, pl. 13, figs. 4a and b

1925 *Diozoptyxis toucasiaephila* Dietrich, p 131

#### Diagnosis

Regular tapering conical shell of moderate thickness. Whorls of moderate height, with a flat or slightly concave profile; either no sutural ramps developed or only very faint ones.

#### Material

BM(NH) GG21830 - GG21834 plus some material examined and photographed in situ.

#### Horizon and Locality

Lower Aptian, Crismina Fort, Sintra Area, Portugal.

#### Description

In addition to the above specific characters, this species shows features typical of the genus. These include a widely hollow columella, bearing pronounced pointed abapical carinae which project into the umbilicus; these carinae become more pronounced as shell size increases (see figure 2.9b). The whorl cross-section (see figure 2.9d) is basically quadratic and shows three strong simple folds (1,1,1,0 fold formula). This species can reach extremely large sizes - specimens up to 220 mm in length have been observed.



Figure 2.9a *Pchelinsevia toucasiaephila* (Dietrich). External morphology. Insitu material. Lower Aptian, Crismina Fort, Portugal.



Figure 2.9b Internal morphology. Insitu material. Lower Aptian, Crismina Fort, Portugal.

### Measurements

Apical Angle:  $21^{\circ}$  (range  $16^{\circ}$  -  $23^{\circ}$ , N = 6)

Sutural Angle:  $104^{\circ}$  (range  $96^{\circ}$  -  $114^{\circ}$ , N = 6)

h/w ratio: 0.30 (range 0.23 - 0.36, N = 4)

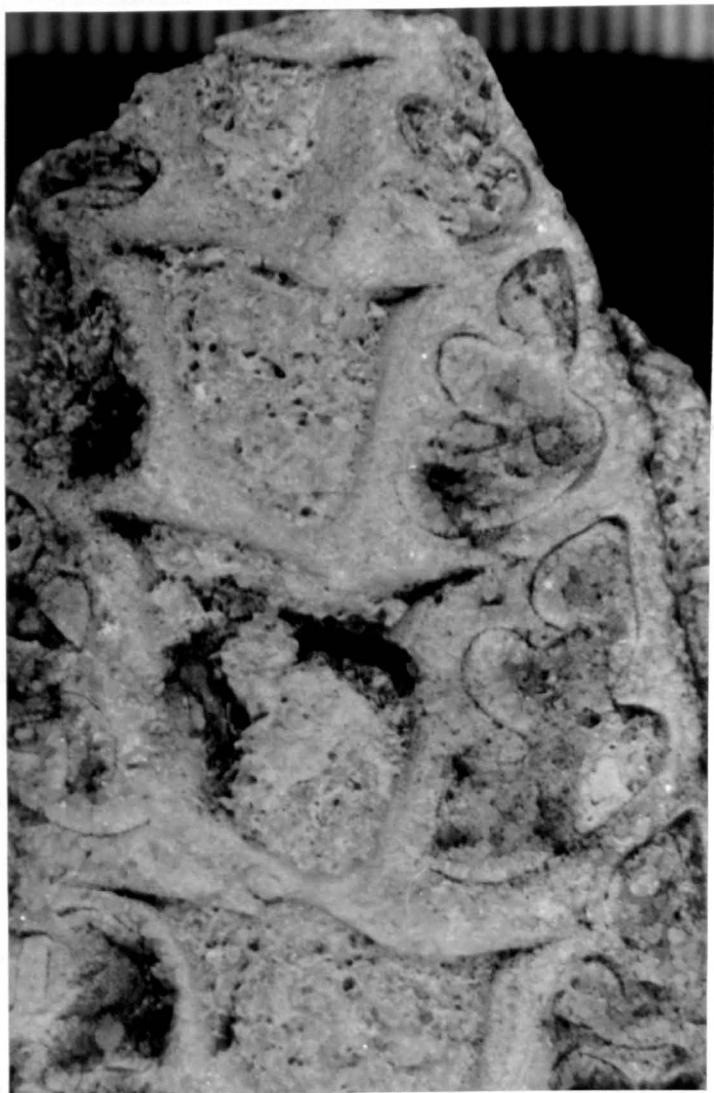


Figure 2.9c *Pchelinsevia toucasiaephila* (Dietrich). Whorl section and umbilical structure. BM(NH) GG21830. Lower Aptian, Crismina Fort, Portugal.

Figure 2.9d Fold pattern in single whorl section. Same specimen as that used in figure 2.9c. Actual whorl height = 8 mm.



### Occurrence

Dietrich (1914) reports this species from three localities in Tendaguru, East Africa. The present author has observed *P. toucasiaephila* at Crismina Fort, Portugal (locality 48).

### Stratigraphical Range

Dietrich (1914) records this species in Urgonian facies of Aptian age (probably Upper Aptian (N. J. Morris, pers comm)). In Portugal, this species occurs in the Calcaires Recifaux Superieurs which is considered to be Lower Aptian in age (Rey, 1979; D. C. Kitson pers, comm).

### Discussion

This species obviously has close affinities with *P. coquandiana*, although the major distinction between the two, the whorl profile, clearly separates them as two distinct species. *P. toucasiaephila* has been reported only from strata of Aptian age, which contrasts with the Hauterivian to Aptian range shown by *P. coquandiana*. The only other report of this species is from East Africa, and its appearance in Portugal may indicate an African influence in this region during Lower Aptian times. The local microfauna also appears to show African affinities (Masse pers. comm.).

*P. toucasiaephila* may represent a predominantly African form of the genus; certainly the absence of reports of this species from the extensively studied Lower Cretaceous strata of Europe implies its geographical range was restricted. Stratigraphical information is at present too limited to draw any firm conclusions regarding the range of this species.

## 2.18.2 *PCHELINSEVIA COQUANDIANA* (d'Orbigny), 1843

(Figures 2.10a,b,c,d)

- \*1843 *Nerinea coquandiana* d'Orbigny, p 75 - 76, plate 156, figures 3 - 4.
- 1843 *Nerinea renauxiana* d'Orbigny, p 76 - 77, plate 157, figures 1 - 4.
- 1862 *Nerinea Renauxiana* d'Orbigny; Pictet and Campiche, p 235 - 236, plate 67, figures 3 (a and b).
- 1862 *Nerinea Coquandiana* d'Orbigny; Pictet and Campiche, p 237 - 238, plate 67, figures 1 (a and b) and 2.
- 1907 *Nerinea (Diozoptyxis) coquandiana* d'Orbigny; Cossmann, p 12 - 13, text figure 3, plate 2, figures 1 - 3 (?figure 4).
- 1907 *Nerinea (Diozoptyxis) renauxiana* d'Orbigny; Cossmann, p 13 - 14, text figure 4, plate 1, figures 6 - 9.
- 1916a *Nerinea (Diozoptyxis) coquandiana* d'Orbigny; Cossmann, p 14 - 15, plate 1, figures 27 - 28.
- 1939 *Nerinea coquandi* d'Orbigny; Delpy, p 180 - 182, plate 4, figures 1 - 5.
- 1965 *Adiozoptyxis cf A. coquandiana* d'Orbigny; Ichikawa and Maeda, p 140 - 141, plate 4, figures 1 (a and b) and 3, ?figure 2.
- 1965 *Diozoptyxis coquandi* d'Orbigny; Pchelintsev, plate 24, figures 2a and b.
- ?1983 *Adiozoptyxis coquandiana* (d'Orbigny); Wen, p 179, plate 1, figures 17 - 18.

### Diagnosis

Conical shell which can vary from coeloconoid to cyrtconoid in shape. Moderate to thick shell. Whorl profile moderately to strongly concave with pronounced sutural ramps bearing coarse tubercular ornament.

### Material

BM(NH) GG 2185 - GG21861



Figure 2.10a *Pchelinesevia coquandiana* (d'Orbigny). External morphology. BM(NH) GG21839. Upper Barremian, Calissane Chateau, France.

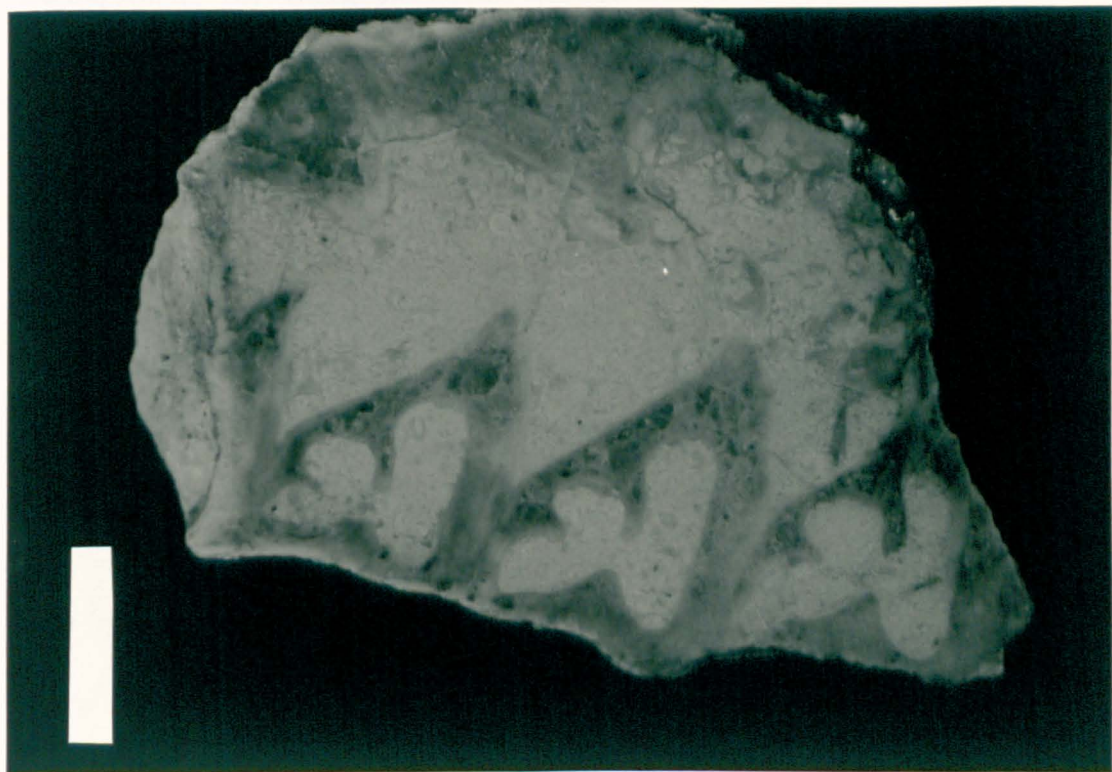


Figure 2.10b Internal morphology. BM(NH) GG21840. Upper Barremian, Calissane Chateau, France.

## Horizons and Localities

Upper Hauterivian, Silicified Locality, S of Crismina, Sintra Area, Portugal. Upper Barremian, Orgon, Brouzet, Calissane Chateau, S of France.

## Description

Sutural ramps can vary considerably in strength. Whorls of moderate height. Whorl cross-section is quadratic to triangular showing three simple strong folds (see figure 2.10c); fold formula is 1,1,1,0. Columella is moderately to widely hollow (ie umbilical width varies considerably). Prominent abapical carinae project into the umbilicus, increasing in strength as shell size increases. Ends of carinae can be rounded or pointed.

## Measurements

Apical Angle:  $23.5^{\circ}$  (range  $20^{\circ}$  -  $28^{\circ}$ , N = 16)

Sutural Angle:  $107^{\circ}$  (range  $98^{\circ}$  -  $114^{\circ}$ , N = 11)

h/w ratio: 0.39 (range 0.32 - 0.50, N = 11)

Whorl concavity index: 0.79 (range 0.73 - 0.83, N = 5)

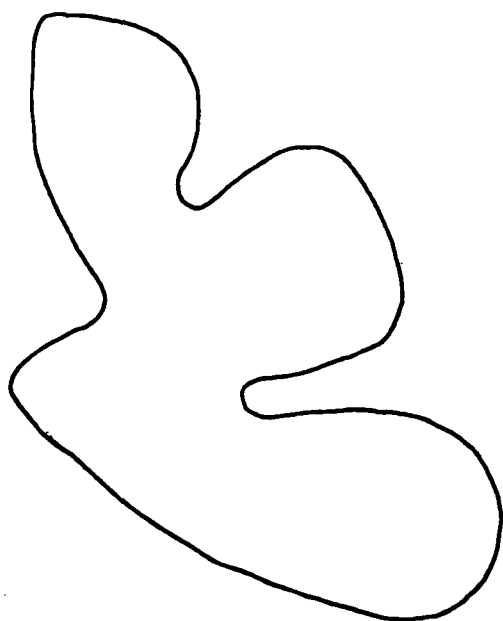


Figure 2.10c *Pchelinsevia coquandiana* (d'Orbigny). Fold pattern in single whorl section. BM(NH) GG21894. Upper Hauterivian, Silicified Locality, Portugal. Actual whorl height = 10 mm.

### Occurrence

This species was extremely widespread within the Tethyan province. In the present study, *P. coquandiana* was observed at a number of localities in southern France and Portugal (localities 7, 17, 25, 45, 60).

### Stratigraphic Range

This species appears to range from the late Hauterivian to at least mid-Aptian (own observations of insitu material, locality 60).

### Discussion

This species appears to have been the most common and widespread representative of *Pchelinsevia*. It has been widely reported in southern Europe and North Africa; also from Pakistan (Ichikawa and Maeda, 1965) and possibly Tibet (Wen, 1983).

*P. coquandiana* can be distinguished from the closely related *P. toucasiaephila* by the occurrence of concave whorls and sutural ramps in the former. *P. coquandiana* also shows a more triangular-shaped whorl cross-section than that seen in *P. toucasiaephila*. However, the overall shape, umbilical morphology and internal fold pattern are almost identical in the two species.

Douvillé (1926, p 354) stated that "*N. coquandi* et *renauxi* ne sont probablement que des variétés d'une même espèce" (*N. coquandi* and *renauxi* are probably no more than varieties of one and the same species). Following this remark, Delpey (1939) formally synonymised *coquandiana* and *renauxiana*, and reported that specimens showed a gradation of characters from one "species" to the other. The amount and quality of the material at present available does not allow a more rigorous testing of this gradation, so Delpey's synonymy has been followed. However, this does mean that a wide range of morphologies are contained within one species - significant variation in whorl profile, sutural ramp morphology, umbilical width (see figure 2.10d) and overall shell shape



occur within the species. Although the case of variation with *D. cochleaeformis* (see Chapter 3) seems to indicate that overall shell shape can vary quite considerably within one species, the degree, extent and type of variations which occur within *P. coquandiana* demand that further consideration should be paid to this species. Should a large number of well-preserved specimens become available, a statistical analysis of shell measurements may help to clarify the situation.

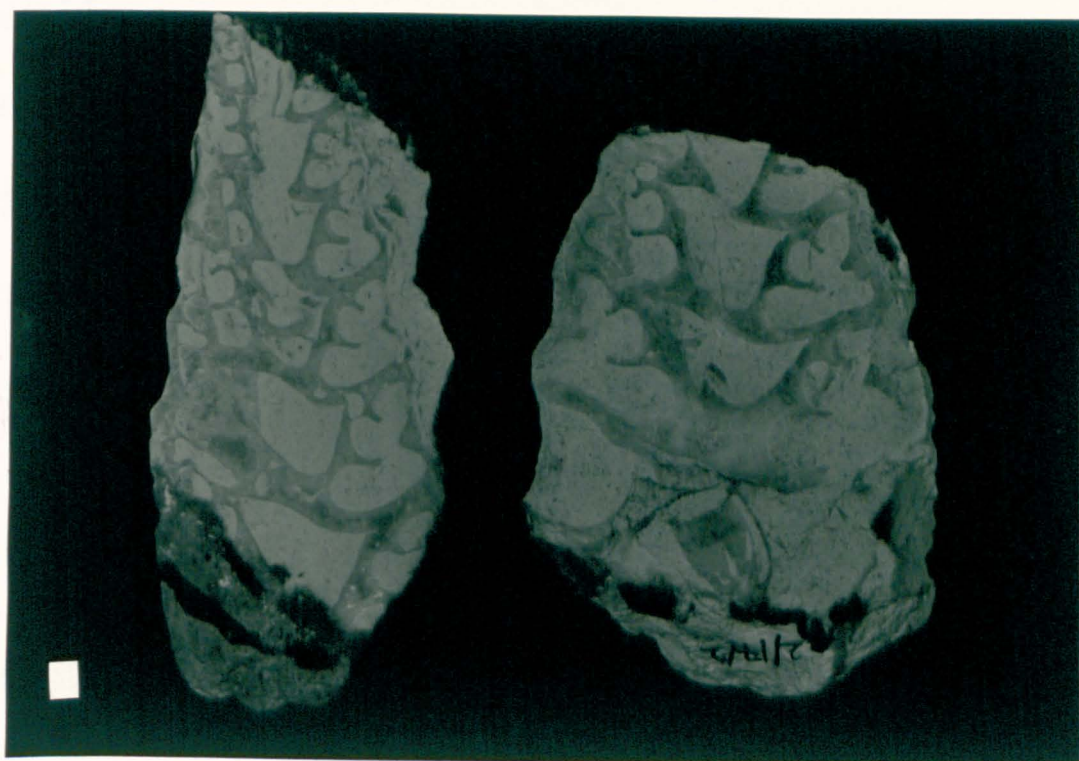


Figure 2.10d *Pchelinsevia coquandiana* (d'Orbigny). Two specimens illustrating the wide range of shell shape and umbilical width currently included within this species. BM(NH) GG21838 (left-hand specimen) and GG21837. Upper Barremian, Brouzet, France (both specimens).

### 2.18.3 *PCHELINSEVIA* species 1

(Figures 2.11a,b)

#### Diagnosis

Widely conical shell with narrow and angular sutural ramps. Extremely wide umbilicus occupying over one-third of overall shell width.

#### Material

BM(NH) GG21929 - GG21932 and GG21998

#### Horizon and Locality

Upper Aptian/Lower Albian, Chodos, Maestrazgo Mountains, NE Spain.

#### Description

Shell shape appears to become more cylindrical as size increases. Whorl profile is concave with pronounced sutural ramps. Fold formula is 1,1,1,0 with fold shape and positioning apparently typical of this genus. This species could reach large sizes; the maximum diameter recorded is 60 mm.

#### Measurements

Apical angle: 25° (N = 1)

Sutural angle: 98° (N = 1)

Whorl concavity index: 0.80 (range 0.78 - 0.81, N = 2)

#### Occurrence

This species has been recognised only from one locality (Chodos, locality 41) in the Maestrazgo Mountains of NE Spain.

### Stratigraphic Range

This species has been found in strata of Upper Aptian or Lower Albian age (Salas, 1984).

### Discussion

The specimens available are rather poorly preserved consisting mainly of internal moulds with only faint traces of internal fold structure preserved. The low quality of the material available precludes the formal erection of a new species.

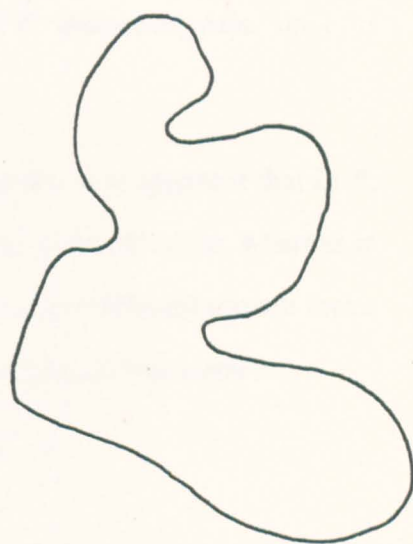


Figure 2.11b Fold pattern in single whorl section. BM(NH) GG21930. Upper Aptian/Lower Albian, Chodos, Spain. Actual whorl height = 17 mm.

Figure 2.11a *Pchelinsevia* species 1. External morphology. BM(NH) GG21932. Upper Aptian/Lower Albian, Chodos, Spain.



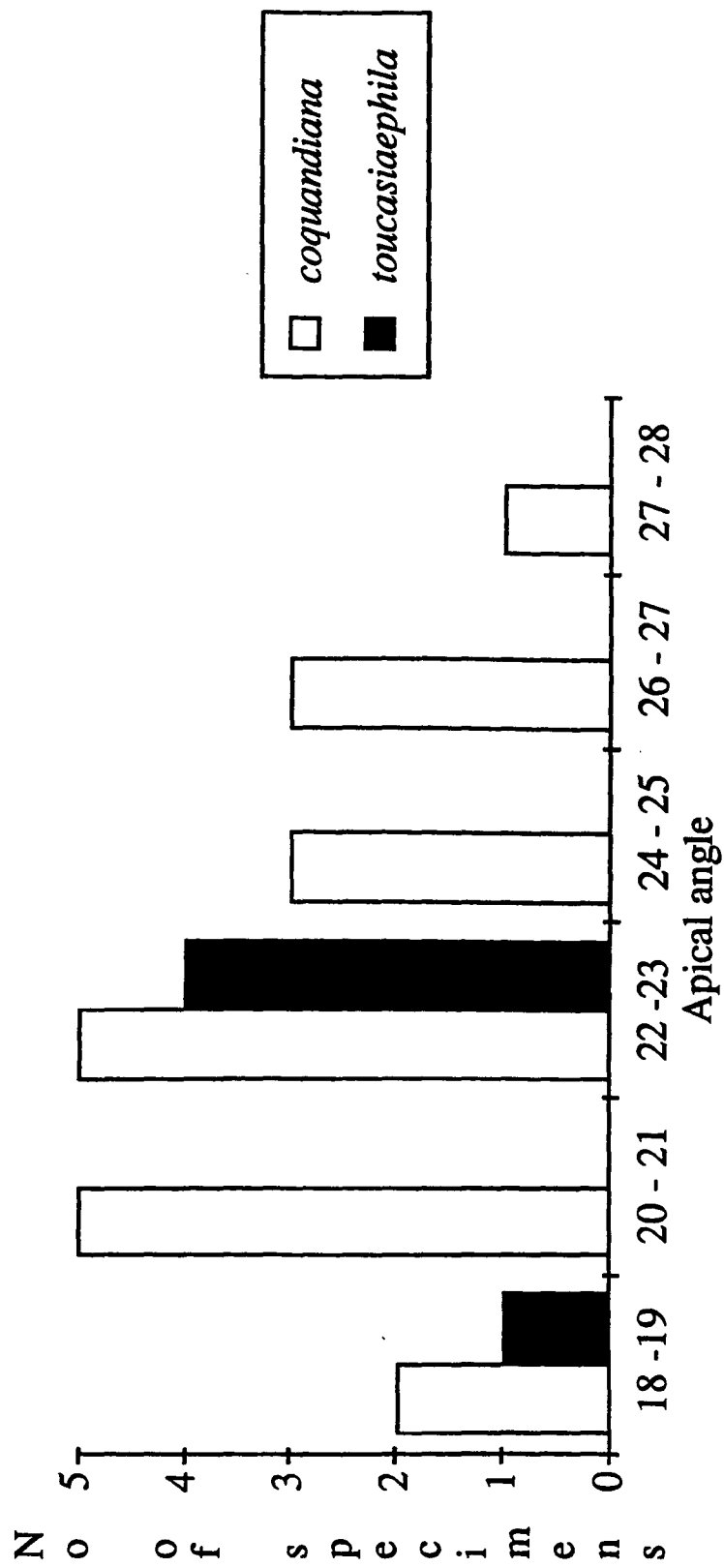
### 2.19 PCHELINSEVIA PARAMETER ANALYSIS

The quantitative parameters given in the species descriptions of *P. toucasiaephila* and *P. coquandiana* are set out graphically in histograms 2.5 to 2.7 and graph 2.2. The raw data used in these plots are given in Appendix 2.

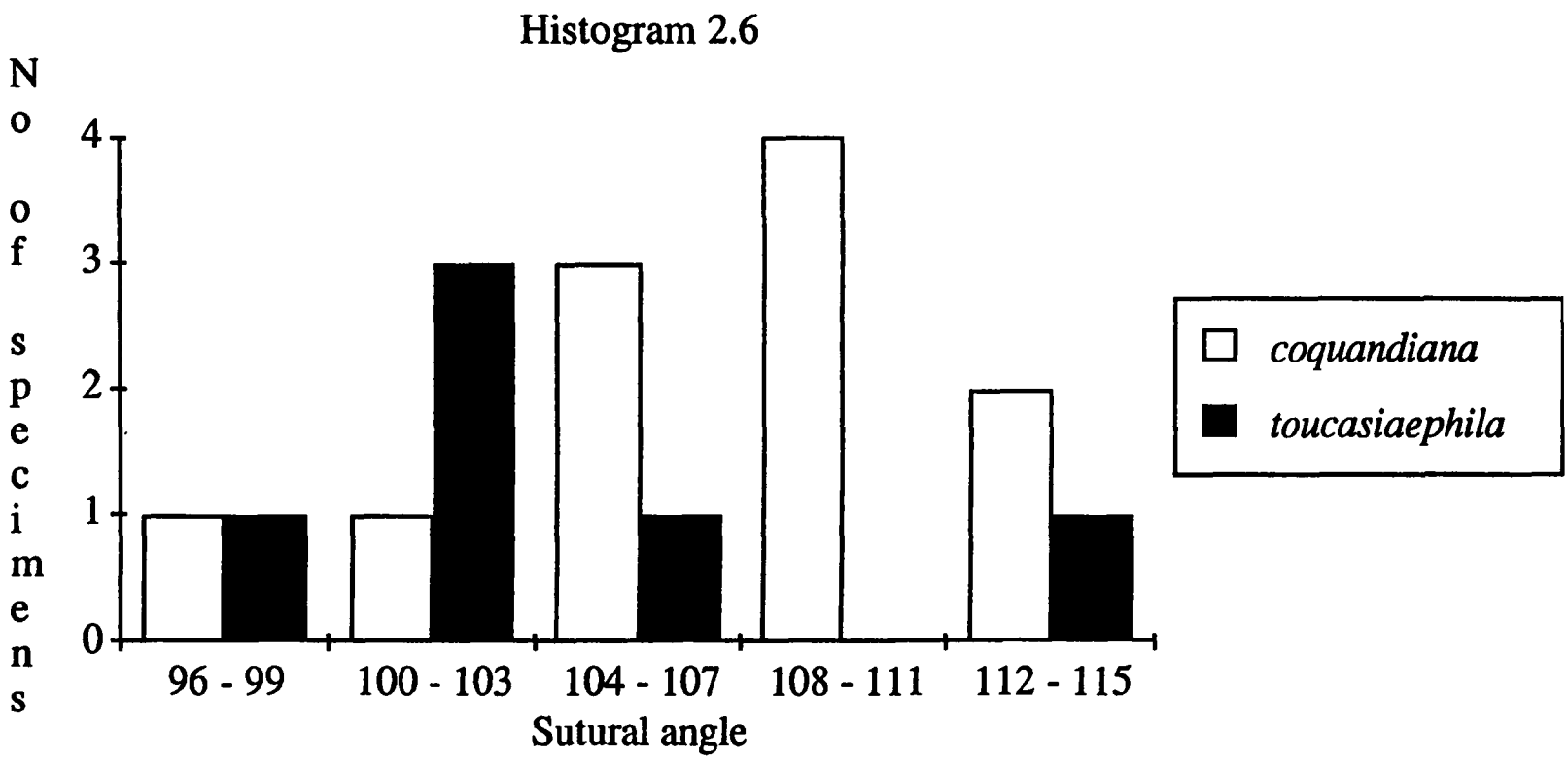
The two species cannot be separated satisfactorily on the three parameters apical angle, sutural angle and h/w ratio as these values show a high degree of overlap. The two species are largely separated on the basis of whorl profile, with the whorl concavity of *P. coquandiana* averaging around 0.79, whereas that of *P. toucasiaephila*, since its whorl profile is flat, is 1.

In graph 2.2, where sutural angle is plotted against h/w ratio, it is apparent that in *P. coquandiana*, h/w ratio is somewhat negatively correlated with sutural angle, whereas in *P. toucasiaephila*, a positive correlation is seen. This may reflect different growth forms in the two species, with *P. coquandiana* showing more cyrtocoid development.

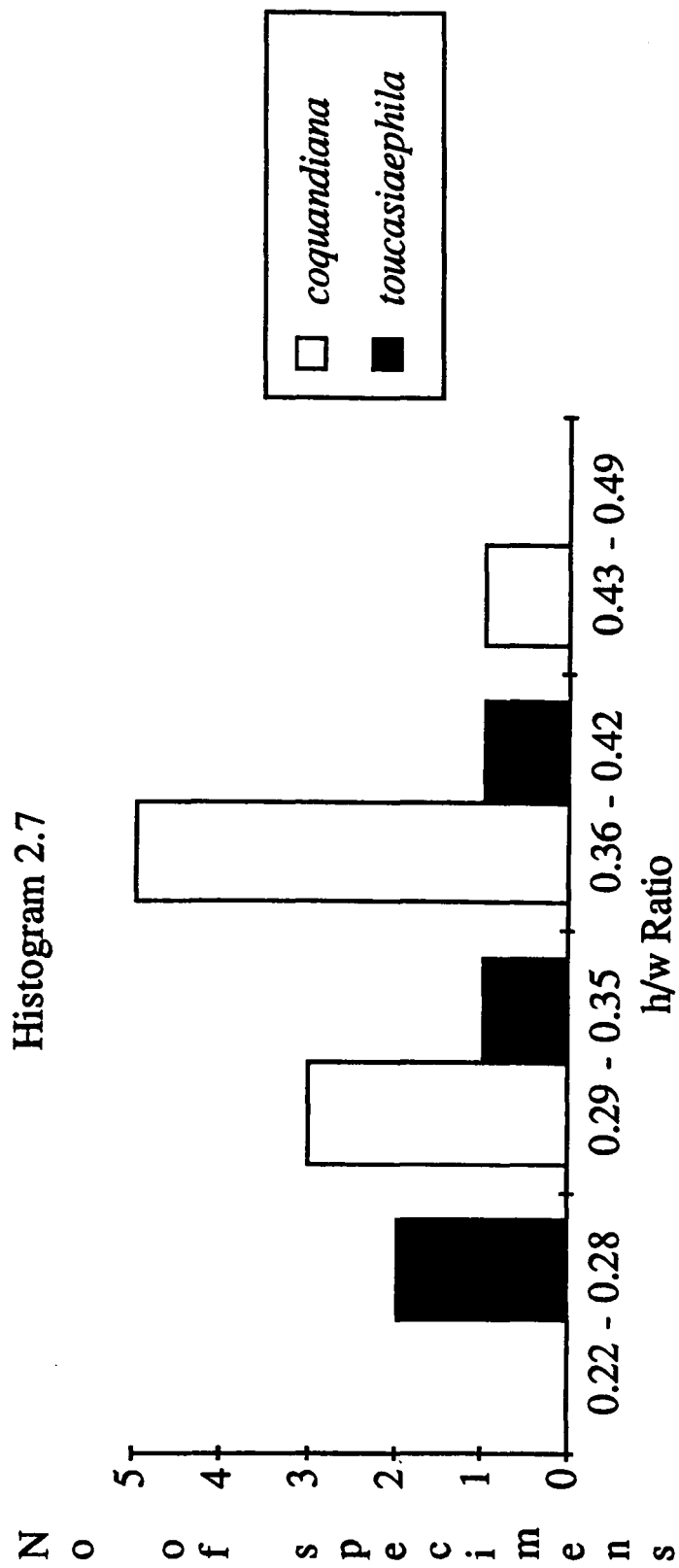
Histogram 2.5



Histogram 2.5 Apical angle measurements in *Pchelinsevia coquandiana* and *P. toucasiaephila*.

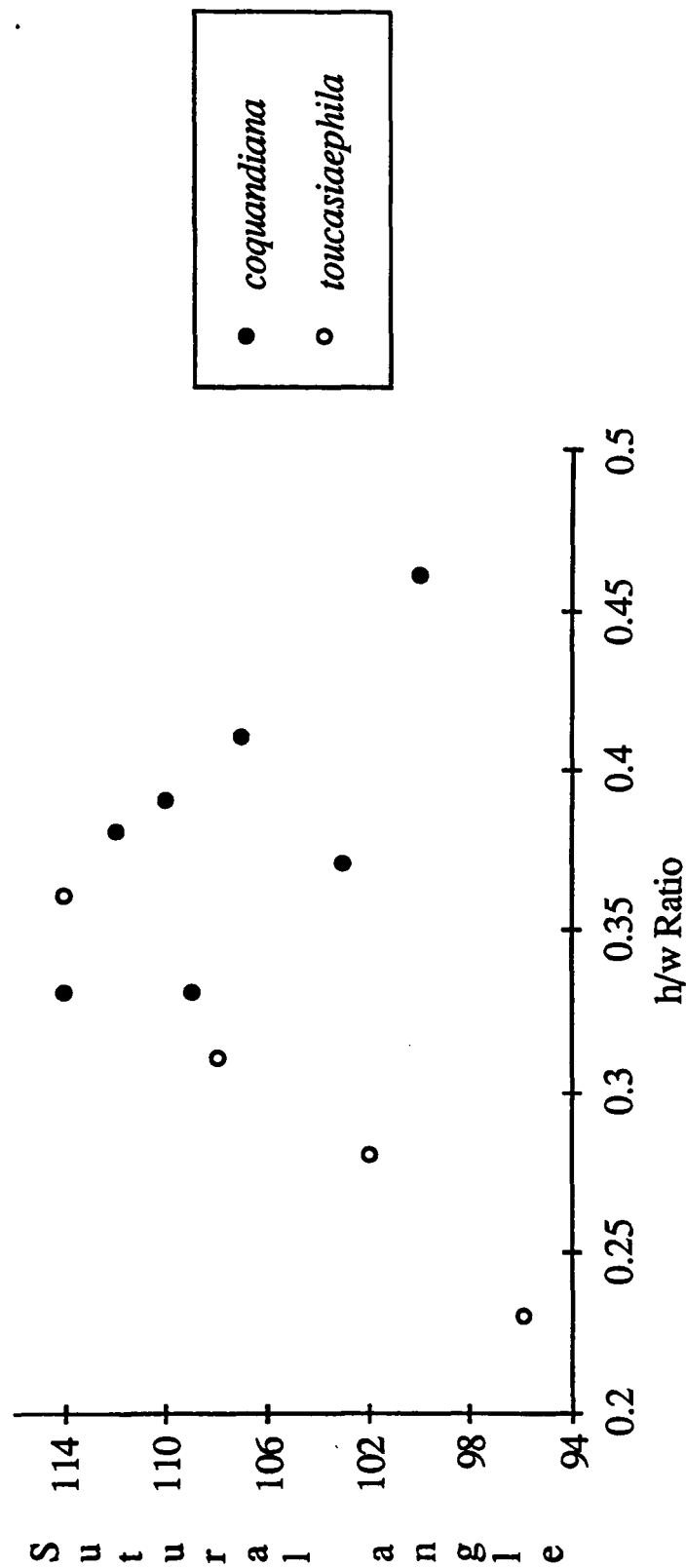


Histogram 2.6 Sutural angle measurements in *P. coquandiana* and *P. toucasiaephila*.



Histogram 2.7 h/w Ratio measurements in *P. coquandiana* and *P. toucasiaephila*.

Graph 2.2



Graph 2.2 Scattergraph of h/w ratio against sutural angle in *P. coquandiana* and *P. toucasiaephila*.

## Incertae subfamiliae

### 2.20 Genus *APHANOPTYXIS* Cossmann, 1896

Type species. By original designation, *Cerithium defrancei* Deslongchamps, 1842.

#### Diagnosis

"Form ... conical, turns concave ... with salient sutures ... umbilical perforation entirely overlapped by columella edge. Opening more or less square ... labrum ... devoid of folds; columella edge ... without lamella or parietal fold"<sup>1</sup>

#### Discussion

This group was set up as a subgenus of *Nerinea* s.l. by Cossmann (1896) with the type species *Cerithium defrancei* Deslongchamps (= *A. langruensis* (d'Orbigny) according to Barker, 1976).

Cossmann clearly defined *Aphanoptyxis* and his diagnosis has largely been accepted by later workers (Dietrich, 1925, Pchelintsev, 1968; Barker, 1976).

Previously, the genus appeared to be restricted to Jurassic strata. The stratigraphic range of *Aphanoptyxis* has been recorded as Bathonian - Rauracian (Cossmann, 1896), Bathonian - Tithonian (Pchelintsev, 1968), and Lower Bathonian - Upper Volgian (Barker, 1977). The species described below therefore considerably extends the known range of this genus.

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<sup>1</sup>"Forme ... conique ... tours concaves ... à sutures saillantes ... la perforation ombilicale est entièrement recouvert par le bord collumellaire. Ouverture à peu près carrée ... labre ... dénué de pli; bord columellaire ... sans lamelle ni pli parietal" Cossmann, 1896, p 35.

The possible affinities of *Aphanoptyx* have been speculated upon by various workers. Pchelintsev (1968) places the genus in the "family Ptygmatisidae" (p 15), apparently on the basis of common conoid shape.<sup>1</sup> However many nerineid genera have conical shells, and as there appear to be no other common features which would imply an association (for example all other "Ptygmatisidae" genera have 4 or 5 folds and an open umbilicus) the association of *Aphanoptyx* with the other genera in this "family" does not appear to be justified.

Barker (1976) comments that Fischer (1969) has placed *Endiaplocus* in *Aphanoptyx* on the basis of similar morphologies (conical shell shape, lack of internal folds etc) including the common occurrence of an umbilicus. Barker disagrees with this suggestion as he has not observed any umbilicate *Aphanoptyx* species and doubts the existence of an umbilicus within the genera. However, Cossmann in his generic diagnosis definitely noted the existence of a "sealed umbilicus". Certainly the sections of specimens of *A. species 1* show small inclusions of sediment within the columella which indicate a narrow space was present, although the actual opening was probably severely restricted by the development of abapical carinae. It therefore seems that at least some *Aphanoptyx* species were narrowly umbilicate. However the extreme conical shape and the very wide umbilicus found in *Endiaplocus* would, in the authors opinion, preclude any close association of this genus with *Aphanoptyx*.

*Aphanoptyx* is a well-defined genus belonging to the Nerineidae; its phylogenetic relationships within this family are at present unclear and it should therefore be regarded as an independent group.

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<sup>1</sup>"Characteristic of this group are the conoid outlines of the shell, the closed umbilicus and the absence of internal spiral folds. These characters unquestionably indicate that this group ..... belongs to the family Ptygmatisidae." (Pchelintsev, 1968, p 16).

### 2.20.1 *APHANOPTYXIS* species 1

(figures 2.12a,b)

#### Diagnosis

Slenderly conical shell with a narrow sutural ramp. Internally a thick columella occupies about 1/3 of total whorl width with a thin umbilicus present in some sections. The whorl cross-section is rounded.

#### Material

BM(NH) GG22074 - GG22079

Geological Survey of Portugal Collection 1148

#### Horizon and Locality

Mid/Upper Barremian, Arriba Pool, N of Crismina, Sintra Area, Portugal.

#### Description

Concave whorls and a sutural ramp symmetrical about the slit-band bearing coarse tubercular ornament. Whorls of moderate height. Where an umbilicus can be seen slight development of abapical carinae is apparent. The whorl cross-section is a slightly elongated square; no folds are present.

#### Measurements

Apical angle :  $16^{\circ}$  (range  $15^{\circ}$  -  $17^{\circ}$ , N = 4)

Sutural angle :  $106^{\circ}$  (range  $103^{\circ}$  -  $109^{\circ}$ , N = 3)

h/w ratio : 0.47 (range 0.35 - 0.57, N = 2)

Whorl concavity index : 0.82 (range 0.78 - 0.86, N = 2)



### Occurrence

This species has only been found in Portugal (locality 47).

### Stratigraphic Range

Mid to Upper Barremian.

### Discussion

The other species assigned to this genus (see Pchelintsev, 1968 and Barker, 1976) are restricted to Jurassic strata of Bathonian to Tithonian age. The discovery of this species in Barremian strata therefore considerably extends the stratigraphic range of the genus.

*A. species 1* conforms well to Cossmann's generic diagnosis and closely resembles two Jurassic species; *A. compressa* Barker (1976, Chapter 2, p 35 -36, plate 2K) although *A. species 1* is more slenderly conical and has a wider columella, and *A. substriata* (d'Orbigny) (d'Orbigny, 1852 p 140 -141, plate 276) - *A. species 1* has lower whorls and a narrower sutural ramp.

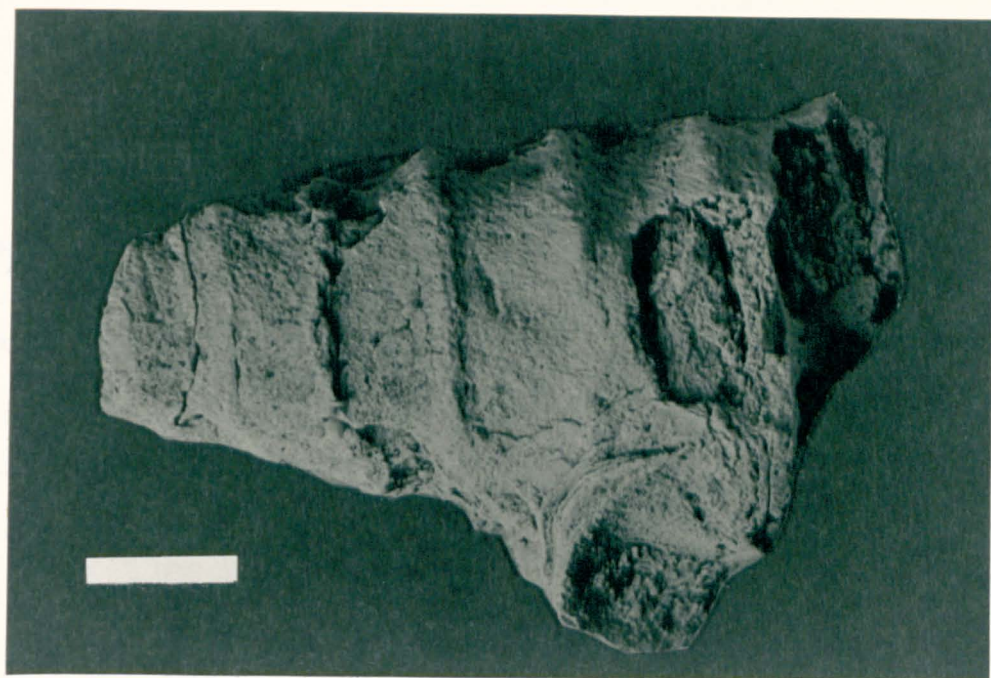


Figure 2.12a *Aphanoptyx* species 1. External morphology with encrusting oyster. BM(NH) GG22079. Mid/Upper Barremian, Arriba Pool, Portugal.

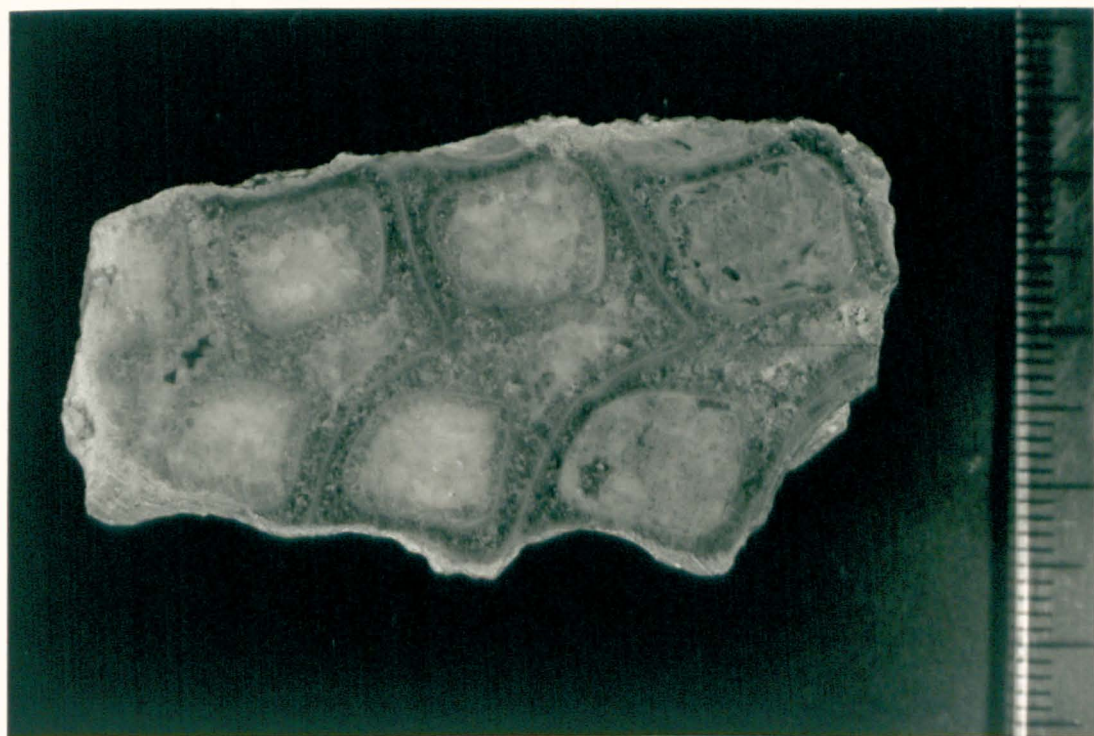


Figure 2.12b Internal morphology. BM(NH) GG22074. Mid/Upper Barremian, Arriba Pool, Portugal.

## 2.21 Subfamily **DIPTYXIDINAE** Pchelintsev, 1965

[name emended and corrected herein ex Diptyxisidae Pchelintsev, 1968]

### Discussion

The Diptyxidinae, consisting of the genera *Diptyxis*, *Cylindroptyxis* and *Oligoptyxis* was erected by Pchelintsev (1965). The former two genera are well-characterised, the main distinctions between the two being in overall shell shape (*Diptyxis* shells are described as conical, whereas *Cylindroptyxis* shells are "semi-cylindrical", p 23), and the solid columella of *Diptyxis* compared to a narrow closed umbilicus in *Cylindroptyxis*.

## 2.22 Genus **DIPTYXIS** Oppenheim, 1889

Type species. By original designation, *Nerinea chsakliana* Herbich, 1886.

### Discussion

*Diptyxis* was set up by Oppenheim (1889, reported in Pchelintsev, 1968, although apparently missed by Wenz, 1940). The genus is described by Pchelintsev as:-

"conically turreted shells, usually with poorly developed sculpture, without umbilicus, with aperture of tetragonal outline and with two simple internal spiral folds (columella and parietal)" Pchelintsev, 1968, p 22

Pchelintsev (1968) records the generic range as Rauracian to Valanginian, so the species described below extends the known range of this genus to at least the Lower Aptian.

### 2.22.1 *DIPTYXIS LUTTICKEI* (Blanckenhorn), 1890

(Figure 2.13a,b)

\*1890 *Nerinea Luttickei* Blanckenhorn, p 106, plate 8, figure 4.

1939 *Nerinea luttickei* Blanckenhorn; Delpey, p 176, text figure 37, plate 3, figures 1 - 2.

(?)1986 *Diptyxis luttickei* (Blanckenhorn); Calzada, p 11, plate 3, figure 4.

#### Diagnosis

Very flat whorl profile with faint swellings at the suture. Columella is slender and solid.

#### Material

BM(NH) GG22062 - GG22067 and, as *D. ?luttickei* GG22080 - GG22081

#### Horizons and Localities

As *D. ?luttickei* from the Mid/Upper Barremian of Arribida Pool, N of Crismina, Sintra Area, Portugal. *D. luttickei* from the Lower Aptian of St Juliao, Ericeira, Portugal.

#### Description

Narrow tapering conical shells with moderately high whorls; no ornament observed. Whorl cross-section is a slightly elongate square shape with two folds (1,1,0,0). The columella fold is wide and long and curves in an adapical direction; the parietal fold is thin and long and curves towards the labrum.

#### Measurements

Apical angle : 14° (range 13° - 15°, N = 4)

Sutural angle : 114° (range 113° - 115°, N = 2)

h/w ratio : 0.59 (range 0.57 - 0.60, N = 2)





Figure 2.13a *Diptyxis luttickei* (Blanckenhorn). External morphology. BM(NH) GG22064. Lower Aptian, St Juliao, Portugal.

#### Occurrence

The present study has recorded this species from Portugal (locality 60); it has also been reported from Lebanon (Blankenhorn, 1890; Delpey, 1939) and also probably from eastern Spain (Calzada, 1986).

#### Stratigraphic Range

*D. luttickei* has been collected from Mid Barremian to Lower Aptian strata.



Figure 2.13b *Diptyxis luttickei* (Blanckenhorn). Fold pattern in single whorl section. BM(NH) GG22062. Lower Aptian, St Juliao, Portugal. Actual whorl height = 9 mm.

### 2.22.2 *DIPTYXIS* species 1

(Figure 2.14a,b,c)

#### Diagnosis

Concave whorls and pronounced rounded sutural ramps of moderate width. Internally there is a thick solid columella.

#### Material

BM(NH) GG22055 - GG22061

#### Horizon and Locality

Lower Aptian, St Juliao, Ericeira, Portugal.

#### Description

Tapering conical shell. A square whorl cross-section showing two long folds (1,1,0,0). The columella fold is wide and curves adapically towards the parietal wall; the parietal fold is very long and curves towards the labrum.

#### Measurements

Apical angle :  $17^{\circ}$  (range  $14^{\circ}$  -  $18^{\circ}$ , N = 3)

Sutural angle :  $111^{\circ}$  (N = 1)

h/w ratio : 0.44 (N = 1)

#### Occurrence

This species has been observed only at St Juliao (locality-60) in Portugal.

#### Stratigraphic Range

Lower Aptian.

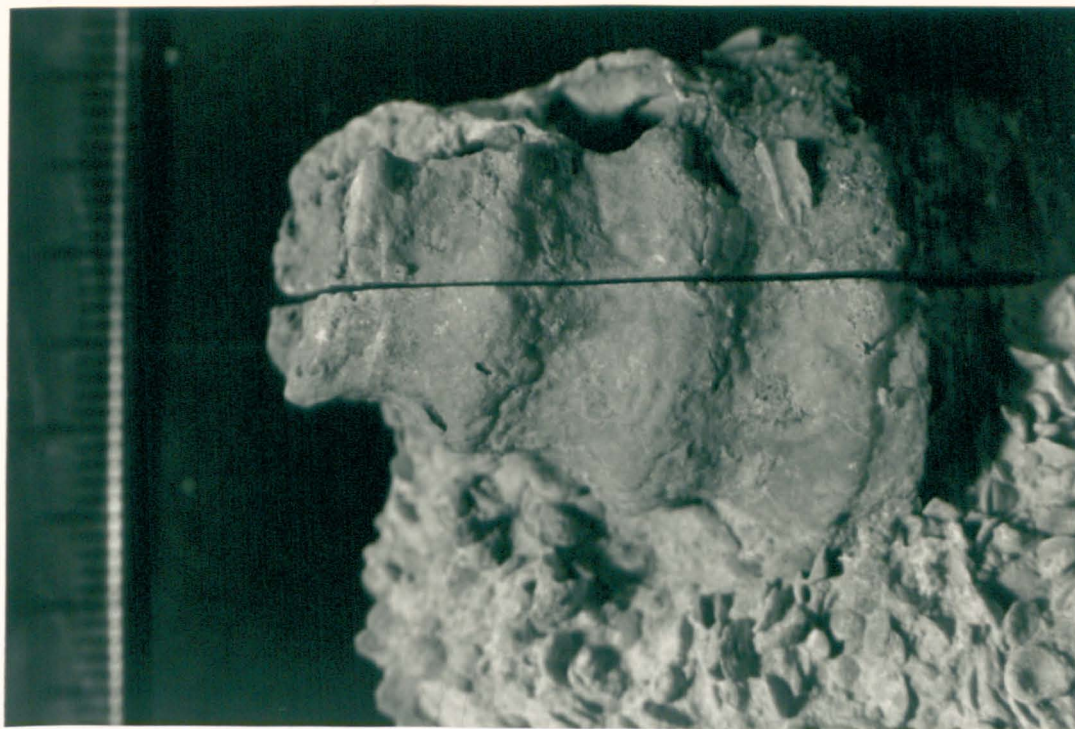


Figure 2.14a *Diptyxis* species 1. External morphology. BM(NH) GG22057. Lower Aptian, St Juliao, Portugal.

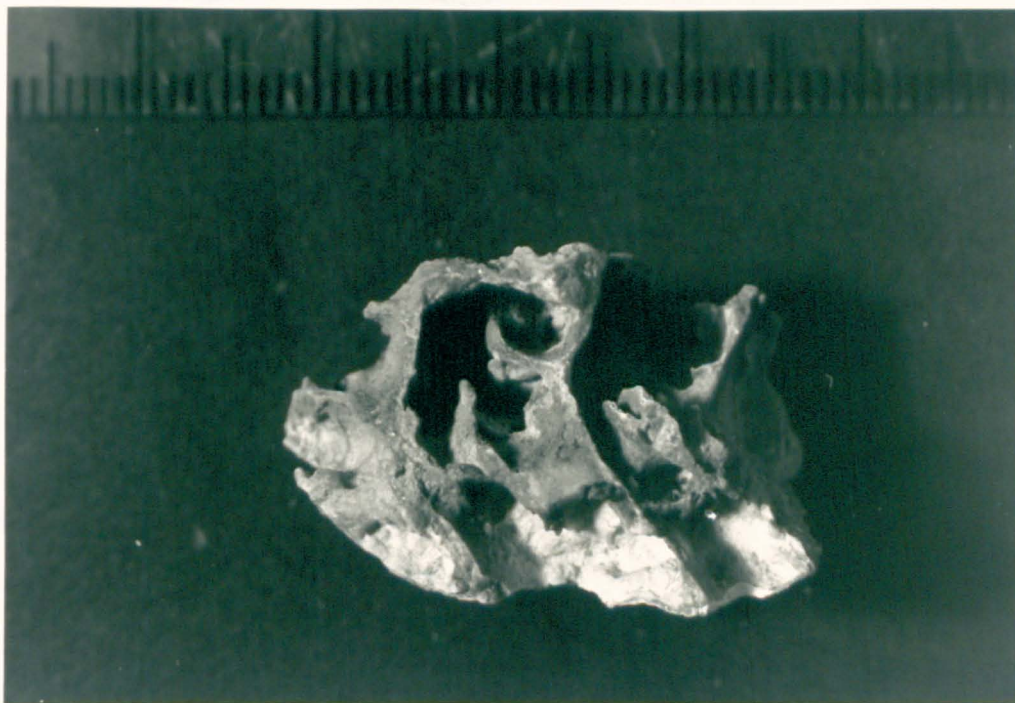


Figure 2.14b Internal morphology in eroded shell section. BM(NH) GG22056. Lower Aptian, St Juliao, Portugal.



## Discussion

This species can be easily distinguished from *D. luttickei* by whorl morphology - the latter has a flat whorl profile, whereas *D. species 1* has concave whorls and sutural ramps. Internally the two species differ in respect of the columella, which is more slender in *D. luttickei*, and also in fold shape, with the folds in *D. species 1* being thicker.

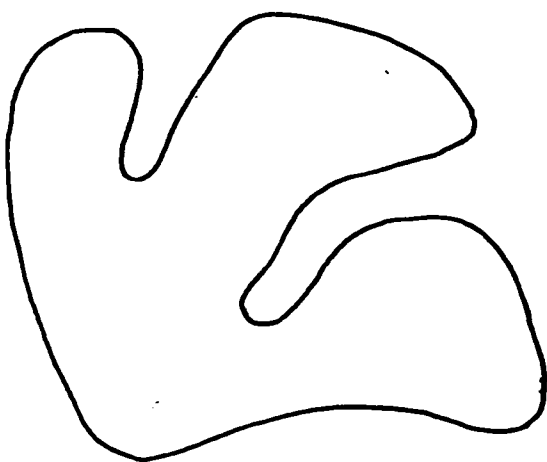


Figure 2.14c Fold pattern in single whorl section. BM(NH) GG22058. Lower Aptian, St Juliao, Portugal. Actual whorl height = 9 mm.

### 2.22.3 *DIPTYXIS* species 2

(Figure 2.15a,b)

.1986 *Cylindroptyxis* species; Calzada, p 8 - 9, plate 3, figure 2.

## Diagnosis

Flat whorl profile. Internally a wide solid columella occupies over 1/3 of overall whorl width. The columella fold is wide, short and rounded.

## Material

BM(NH) GG22052 - GG22054



### Horizon and Locality

Upper Hauterivian/Lower Barremian, (locality 46) S of Crismina, Sintra Area, Portugal.

### Description

Stoutly conical shell. Moderately long abapical canal terminating aperture. Whorl cross-section is almost square with a very slight tendency for later whorls to cover the preceeding ones (see figure 2.15a). There are two strong simple folds (1,1,0,0); the parietal fold is wide and long and curves towards the labrum.



Figure 2.15b Fold pattern in single whorl section. Same specimen as that in 2.15a.

Figure 2.15a *Diptyxis* species 2. Internal morphology. BM(NH) GG22054. Lower Barremian, locality 46, S of Crismina, Portugal.

### Measurements

Apical angle : 16° (range 15° - 18°, N = 3)

### Occurrence

Calzada reports the species from Ares de Maestre, Castellón province, eastern Spain; the present study has found this species only at one locality (46) in Portugal.

### Stratigraphic Range

Hauterivian to Lower Barremian.

### Discussion

This species conforms well to the generic diagnosis of *Diptyxis* (especially when compared with the type species of the genus); the association of *D.* species 2 with *Cylindroptyxis* (Calzada, 1986) does not therefore appear to be justified.

Calzada (1986) reports that Alencaster (1956) has described an unnamed *Nerinea* species which is very similar to this species from the Lower Cretaceous of Mexico.

## Incertae subfamiliae

### 2.23 Genus *JULESIA* Cox, 1954

[= *Favria* Cossmann, 1916 non Tutt, 1906]

Type species. By original designation, *Phaneroptyxis pellati* Cossmann, 1907.

### Revised Diagnosis

Shell form varies from stoutly conical to extremely stoutly conical. Apparent apical angle increases markedly when overall shell length is between 5 - 10 mm. The apical

part of the shell is therefore more slender than later adapical whorls, giving an unusual shell shape - a pointed narrow apex with a bulging conical adapical shell developing later. The change in apparent apical angle is accompanied by a change in whorl height from low to moderate. Whorl profile is concave, with rounded sutural ramps bearing coarse tubercular ornament. Internally, the columella is either solid or extremely narrowly umbilicate. Whorl cross-section is quadratic, with a 1,1,0,0 fold pattern; later whorls tend to overlap preceeding ones slightly ( up to  $\frac{1}{4}$  of preceeding whorl height).

### Discussion

Cossmann (1916a, p 14) erected "*Favria*" with the type species *Phaneroptyxis pellati* Cossmann. Cox (1954) apparently discovered that the name proposed by Cossmann had already been used in a different context, and was therefore unavailable. Cox proposed a new name, *Julesia*, for the group. Cox did not comment on the characteristics of *Julesia*, presumably accepting Cossmann's diagnosis of the group. However, this diagnosis (Cossmann, 1916, p 14) is somewhat misleading and incomplete. A revised diagnosis is therefore proposed above.

*Julesia* is distinctive, but apparently quite rare, with only a few species; *J. pellati*, *J. cureti* Cossmann and *Nerinea (?) sphinxi* Favre (reported by Cossmann, 1916a). If the latter species is included, the stratigraphic range of the genus extends from the Lower Portlandian to the Upper Barremian.

The ontogenetic change in shell form shown by *Julesia* is unusual in the Nerineacea, although other marked ontogenetic changes occur in other genera, for example, the disappearance of spiral ornament in *?Polyptyxisella schicki* (section 2.27.1).

Cossmann (1916a) included *Julesia* (= *Favria*) as a subgenus of *Phaneroptyxis*, thereby placing the group in the Itieriidae. Although the tendency for whorls to overlap is characteristic of the itieriids, it occurs to only a slight extent in *Julesia*. The author

considers that the overall shell morphology of this genus conforms to placement within the Nerineidae.

### 2.23.1 *JULESIA PELLATI* (Cossmann), 1907

(Figure 2.16a,b,c)

\*1907 *Phaneroptyxis pellati* Cossmann, p 8 and 9, text figure 1, plate 1, figures 10 and 11, plate 2, figures 9 - 12

1916a *Phaneroptyxis (Favria) Pellati* Cossmann, p 13 and 14, plate 1, figures 21 - 26

1916b *Favria pellatii* Cossmann, p 348 and 349, plate 10, figures 13 and 14

#### Diagnosis

Whorl profile is very concave with wide rounded bulging sutural ramps. Internally, a thick columella occupies over 1/4 of total whorl width.

#### Material

BM(NH) GG22043 - GG22047

Collection Curet, Laboratory of Invertebrate Palaeontology, Université de Paris VI  
(Pierre et Marie Curie) Drawer 7144

#### Horizons and Localities

Upper Hauterivian, Silicified Locality, S of Crismina, Sintra Area, Portugal. Upper Barremian, Brouzet, Calissane Chateau, S of France.





Figure 2.16 *Julesia pellati* (Cossmann). External morphology. BM(NH) GG22046. Upper Barremian, Brouzet, France.



Figure 2.16b Internal morphology. BM(NH) GG22044. Upper Barremian, Calissane Chateau, France.

### Description

Stout conical shells which show a high rate of whorl width expansion and irregular growth form. Sutural ramps bear light large scale tubercular ornament. The slit-band occurs as a marked depression in the centre of the ramp. A very narrow umbilicus may develop as shell size increases, but often the columella appears solid. Later whorls tend to overlap preceeding ones. Whorl cross-section is quadratic with two folds (1,1,0,0) both of which are long and thin; columella fold curves in an adapical direction.

### Measurements

Apical angle :  $16^{\circ}$  (range  $15^{\circ}$  -  $16^{\circ}$ , N = 4) - the markedly irregular growth shown by this species means that the apparent apical angle varies considerably during ontogeny - these figures were obtained from the earliest whorls

Sutural angle:  $103^{\circ}$  (range  $102^{\circ}$  -  $105^{\circ}$ , N = 3)

h/w ratio : 0.43 (range 0.41 - 0.46, N = 3)

Whorl concavity index : 0.74 (range 0.63 - 0.85, N = 4) - degree of whorl concavity shows considerable variation in this species.

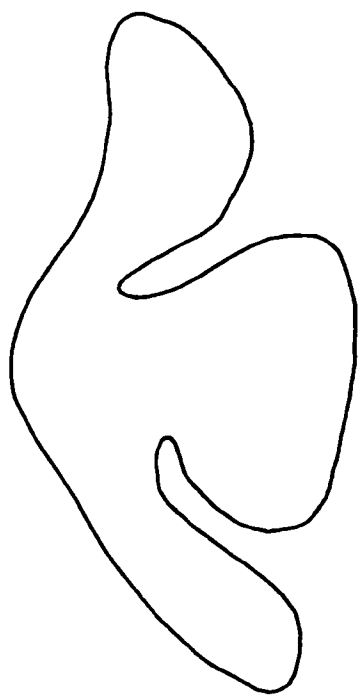


Figure 2.16c *Julesia pellati*  
(Cossmann). Fold pattern in single  
whorl section. BM(NH) GG22044.  
Upper Barremian, Calissane Chateau,  
France. Actual whorl height = 10 mm.

### Occurrence

This species appears to be widespread in southern France (Cossmann, 1907; 1916a and b; localities 7, 17) and has also been found in Portugal (locality 45).

### Stratigraphic range

*J. pellati* has been collected from strata ranging in age from the Upper Hauterivian to Upper Barremian.

### Discussion

This species is rather unusual in that overall shell shape appears to vary quite considerably as a result of different rates of whorl width expansion which give rise to a range of apical angles; variation in whorl concavity is also apparent. This variation can also be seen in Cossmann's figures (particularly apparent in De Brun et al, 1916, plate 1, figures 21 - 26).

Cossmann (1916a) also reports some specimens of "*F. pellati* " with two folds (1,1,0,0) (also figured in Cossmann, 1907, p 8), and some with three (1,1,1,0). He discusses this range in morphology, which is attributed to sexual differences<sup>1</sup>. If the opisthobranch affinities of the Nerineacea are accepted (see chapter 6) then another explanation of this variation is necessary, as opisthobranchs are hermaphrodite (Fretter and Graham, 1962).

The range in morphology may be a characteristic of this species, or possibly more than one species are currently being combined together. Certainly the reported difference in fold number (all the specimens examined in the present study had only two folds) would

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<sup>1</sup>"je ne puis attribuer qu'a une différence de sexe l'aspect absolument différent de ces groupes d'échantillons" Cossmann, 1916, p 13.

definitely indicate different species and probably different genera. Unfortunately, *J. pellati* appears to be quite rare, especially when compared to the number of specimens of other species found at the same localities; it has therefore proved impossible to test whether the morphological variation is continuous or discontinuous.

## Family ITIERIIDAE Cossmann, 1896

### Incertae subfamiliae

#### 2.24 Genus *PHANEROPTYXIS* Cossmann, 1896

Type species. By original designation, *Nerinea moreana* d'Orbigny, 1841.

#### Revised Diagnosis

Ovo-conical shell shape, slightly convex whorl profile with slight sutural ramps bearing faint tubercular ornament. The height of the last whorl is equal to or greater than half the overall shell length. Internally, the columella is narrowly umbilicate, but can appear solid due to infilling by abapical carinae. Later whorls envelop earlier ones, covering about 2/3 of the preceeding whorl height. Whorl cross-section is elongate, with three strong folds, 1,1,1,0.

#### Discussion

This genus has largely been accepted as representing a discrete phylogenetic unit (Wenz, 1940; Pchelintsev, 1968) although neither the original diagnosis given by Cossmann, nor those subsequently developed (Wenz, 1940; Pchelintsev, 1968) are satisfactory. A revised diagnosis is therefore given above.



The ovate shape and enveloping whorls of *Phaneroptyxis* suggest affinities with *Itieria* and *Vernedia*; the genus is therefore placed in the Itieriidae, although it may represent a phylogenetic link between the Nerineidae and Itieriidae (see Chapter 5).

#### 2.24.1 *PHANEROPTYXIS AFRICURGONIA* Dietrich, 1914

(Figure 2.17a,b,c)

\*1914 *Phaneroptyxis africurgonia* Dietrich, p 146, 147, text figures 4 and 5 Plate 11, figure 26 (a, b and c)

##### Diagnosis

Bulging convex whorls bearing coarse tubercular ornament below line of whorl contact. Whorl height is rather low compared to other members of the genus.

##### Material

BM(NH) GG22088 - GG22104

##### Horizon and Locality

Lower Aptian, Lagarde d'Apt, S of France.

##### Description

Stoutly conical shell. No sutural ramp but a depression in the area of whorl contact. Short canal terminates aperture abapically. Internally a moderately thick columella occupies over 1/4 of total whorl width. The shell is narrowly umbilicate with the hollow columella space virtually filled by rounded abapical carinae. Later whorls tend to curve adapically and cover approximately one half of the total height of the preceding whorls.



Figure 2.17a *Phaneroptyxis africurgonia* Dietrich. External morphology. BM(NH) GG22099. Lower Aptian, Lagarde d'Apt, France.

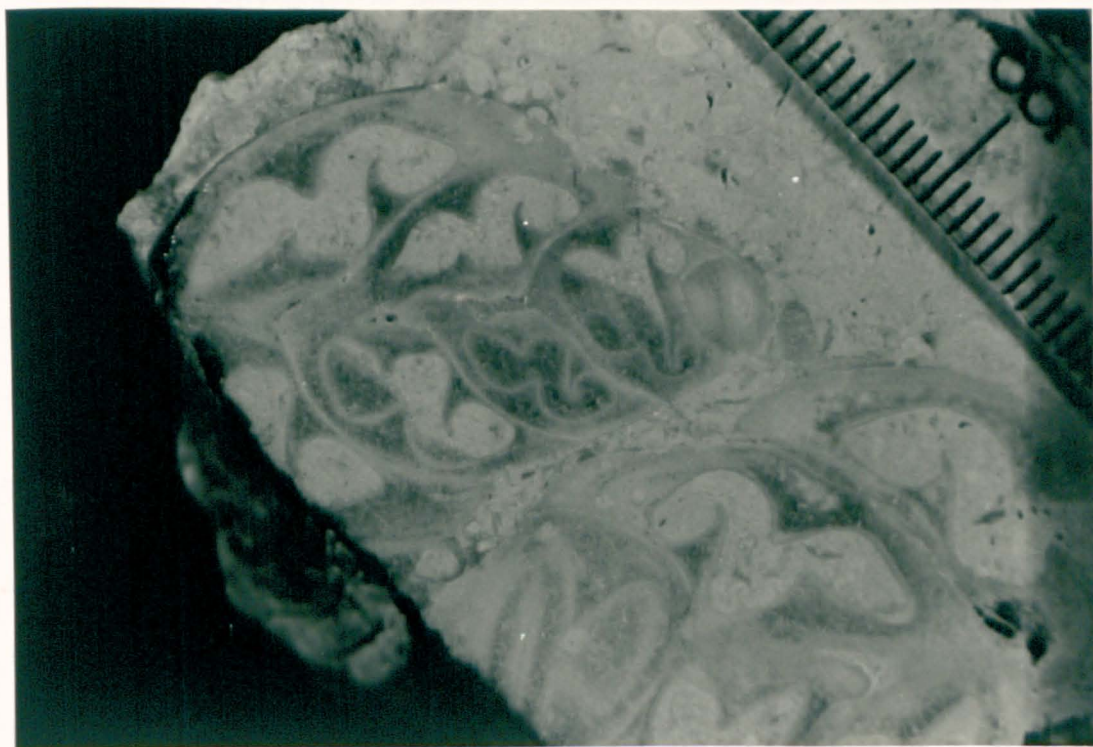


Figure 2.17b Internal morphology. BM(NH) GG22103. Lower Aptian, Lagarde d'Apt, France.

Whorl cross-section is a rounded diamond shape with three folds (1,1,1,0 - see figure 2.17c)

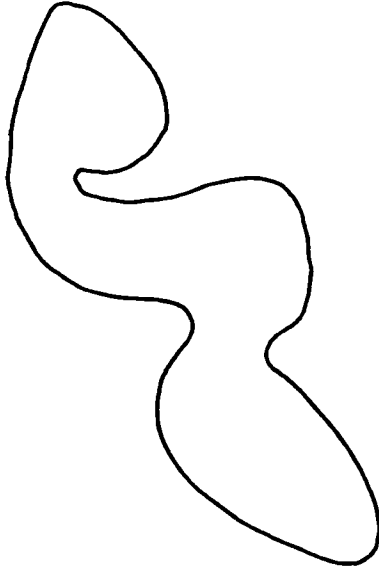


Figure 2.17c *Phaneroptyxis africurgonia*  
Dietrich. Fold pattern in single whorl  
section. BM(NH) GG22103. Lower  
Aptian, Lagarde d'Apt, France. Actual  
whorl height = 7 mm

### Measurements

Apical angle :  $15.5^{\circ}$  (range  $14^{\circ}$  -  $18^{\circ}$ , N = 4)

Sutural angle :  $95^{\circ}$  (range  $92^{\circ}$  -  $98^{\circ}$ , N = 3)

Whorl concavity index: 1.21 (range 1.17 - 1.25, N = 2) - whorls in this genus are convex

### Occurrence

This species has only been reported from East Africa (Dietrich, 1914) and Lagarde d'Apt, southern France (locality 34).

### Stratigraphic Range

Dietrich reports the species from Urgonian facies of Aptian age; specimens collected by the author were in Urgonian limestone of Lower Aptian age.

### Discussion

Dietrich's specimens of this species appear to be somewhat smaller than those found in southern France.

## 2.25 Family NERINELLIDAE Pchelintsev, 1965<sup>1</sup>

### Discussion

Pchelintsev (1968) created a new superfamily, the "Nerinellacea", containing the Nerinellidae and seven other new families. Together these families contain 18 genera, 14 of which have been erected by Pchelintsev including 10 new genera. The changes proposed by Pchelintsev are therefore extensive and will need careful evaluation. Detailed analysis of Pchelintsev's suggestions is likely to be severely hampered in respect of the seven genera which contain almost exclusively species known only from the Crimean-Caucasian areas.

The creation of the superfamily Nerinellacea does not appear to be justified. It is one aspect of Pchelintsev's overall approach involving the elevation of families to superfamilies contained within a new order the Murchisoniata. Pchelintsev does not explain his reasons for elevating these families; it seems to be an unnecessary attempt to "tidy up" the taxonomic situation which has not been considered in scientific terms.

Full consideration of Pchelintsev's treatment of this group has not been within the scope of the present study. However, some general observations can be made. It does seem that extremely acicular-shelled genera within the Nerineacea could usefully be grouped together as a family. A parallel situation can be seen in the Itieriidae which contains ovate nerineids. Acicular nerineids are among the very earliest known representatives of the group (Dietrich, 1925), but, although several workers (Cossmann, 1896; Dietrich, 1925) have noted a "parallelism" in fold patterns between acicular-shelled species and those with more cylindrical or conical shells, the absence of intermediate forms (in terms of gross morphology) would tend to confirm an early phylogenetic separation of the

---

<sup>1</sup>Pchelintsev records "Family Nerinellidae Zittel emend Pchelintsev" (1968, p 26), however Zittel did not erect a family Nerinellidae; the authorship of this family belongs exclusively to Pchelintsev.

acicular group. After this divergence, it is envisaged that, for some unknown reason certain fold patterns were "stable" for nerineacean animals, whatever their overall shell shape (see Chapter 5). If acicular nerineids had repeatedly evolved into or from more conventionally shaped taxa, a number of intermediate shell forms would be expected. The present study has not encountered any such "transitional" forms, although it should be noted that the Mid-Jurassic would be the most likely strata to show such forms. Cox (ms circa 1953) states "it is not always easy to decide where to draw the limit between *Nerinella* and *Cossmannea*" but Barker (1976) while working on Bathonian assemblages, reported little difficulty in distinguishing *Nerinella* species using apical angle and whorl height/width ratios as the main distinguishing criteria. A detailed study of the stratigraphic ranges and morphology of late Lower Jurassic and Mid Jurassic nerineids would clarify the situation. However, it appears that Pchelintsev's creation of Nerinellidae allows a convenient separation of acicular shelled nerineids and may well reflect a true phylogenetic divergence.

#### 2.25.1 Taphonomy of the Nerinellidae

The elongate and slender shape of these shells means that they are usually poorly preserved. Unbroken specimens are rare, and often, unless preserved in fine-grained deposits which accumulated slowly, the sediment did not penetrate far "up" (ie apically) the whorls, with the result that the internal structure has usually been obliterated by the development of crystals in the whorl cavity during recrystallisation. Barker (1976) has made a thorough study of the various taphonomic processes which may affect preservation in nerineid shells.

In addition to taphonomic problems, the shape of the shells makes it difficult to obtain median sections without destroying at least half the shell and risking breakage to the remaining half. The group therefore offers particular difficulties for palaeontologists, unless particularly good preservation conditions prevailed.

## Incertae subfamiliae

### 2.26 Genus *NERINELLA* Sharpe, 1849

[= *Nerinoides* Wenz, 1940]

Type species. By subsequent designation (Cossmann, 1896, p 36), *Nerinea dupiniana* d'Orbigny, 1843.

#### Discussion

Sharpe (1849) proposed *Nerinella* as a subgenus of *Nerinea* sl but failed to specify a type species for the group, although he did include 10 nerineid species within it. The type species of *Nerinella* ss was subsequently designated (ICZN 1985, Article 69a) by Cossmann (1896, p 36) as *N. dupiniana* (d'Orbigny).

Cossmann also elevated *Nerinella* to full generic status and included 3 sub-genera - *Nerinella* ss, *Bactroptyxis* Cossmann and *Aptyxiella* Fischer. Sharpe's group had not been well-received by other workers, and Cossmann hoped his revised diagnosis would enable *Nerinella* to become more widely accepted. The main elements of Cossmann's diagnosis included:-

"acicular shell, pointed spire ..... narrow rhomboidal opening and one to three internal folds depending on the degree of salience shown"<sup>1</sup>

Cossmann (1896) reports that d'Orbigny's (1843) figure of *N. dupiniana* (reproduced by Sharpe, 1849) lacked its "pli columellaire antérieur" (p 37) (anterior columella fold). This indicates that *N. dupiniana* possesses three folds (1,1,1,0) and therefore this fold

---

<sup>1</sup>"Forme aciculée; spire pointue .....ouverture ..... toujours rhomboidale;.....trois plis paraissant quelquefois se réduire à deux ou même à un seul, par suite d'une saillie insuffisante de l'un ou de deux d'entre eux." Cossmann, 1896 p 36.

pattern should be considered a generic character. The author does not consider that species with different fold numbers should be placed together in the same genus (see Chapter 5). *Nerinella* should therefore be restricted to appropriate species with a 1,1,1,0 fold pattern, and other morphologically similar species with other fold patterns must be considered to belong to other genera.

Subsequent authors (Dietrich, 1925; Wenz, 1940; Pchelintsev, 1968; Barker, 1976) appear to have largely accepted Cossmann's interpretation of the group, although Wenz (1940) attempted to rename the group "*Nerinoides* Wenz" because he considered the name *Nerinella* had been previously validly used by Nardo in 1847. However, an application was made by Cox to the ICZN on this point which ruled (Opinion 316, 1954) that *Nerinella* Nardo was a nomen nudum, leaving *Nerinella* Sharpe as a valid name, and *Nerinoides* Wenz a junior objective synonym of *Nerinella*.

### 2.26.1 *NERINELLA ALGARBIENSIS* Choffat, 1887

(Figures 2.18a,b,c)

\*1887 *Nerinella algarbiensis* Choffat, p 288.

v.1901 *Nerinella algarbiensis* Choffat, p 121, 122, plate 4, figures 1 - 8

#### Material

BM(NH) GG22014

Geological Survey of Portugal Collection 1164 - 1166 (NB these specimens were all figured by Choffat (1901))

#### Horizon and Locality

Aptian, Praia da Luz, Algarve, Portugal.





Figure 2.18a *Nerinella algarbiensis* Choffat. Large block containing many specimens showing external and internal morphology. BM(NH) GG22014. Aptian, Praia da Luz, Portugal.



Figure 2.18b Internal structure. Detail of same material as that in figure 2.18a.



## Discussion

This species was collected from the same locality as that given by Choffat (1901), (locality 68 - see appendix), just west of Praia da Luz, near Lagos, Southern Portugal. Choffat has fully described and figured *N. algarbiensis*.

Delpey (1939, p 156 - 157) has synonymised Choffat's species with *Nerinella utrillasensis* Verneuil and Lorient (1868, p 16, plate 2, figure 16). However, Choffat (1901) discussed *N. algarbiensis* in relation to *N. utrillasensis*, stating that the two could be distinguished on the basis of *N. utrillasensis* having lower and more concave whorls ("*N. utrillasensis* Verneuil et Lorient ..... a les tours moins hauts et beaucoup plus concaves" (p 121, 122)). Delpey (p 157) states:- "*N. algarbiensis* a même coupe et sans doute même forme extérieure que *N. utrillasensis*" (*N. algarbiensis* has the same section and without doubt the same external form as *N. utrillasensis*). However, she figures (p 157, figures 114 and 115) "adult" shells which show a concave whorl profile and narrow sutural ramps, while "young" individuals are shown (p 157, figures 112 and 113) with a virtually straight whorl profile. This is exactly the opposite of Choffat's description (p 121) "tours excavés dans la jeunesse, devenant plus tard plans, ou à peu près" (early whorls concave, later becoming more or less flat). Choffat's figures (plate 4, figures 1 - 8), his specimens (Geological Survey of Portugal Collection 1164, 1165 and 1166) and the author's own specimens (BM(NH) GG22014 - a large block containing many shells) confirm that this species has only slightly concave whorls during early ontogeny, with the whorl profile becoming virtually flat as growth progresses. Therefore Delpey's synonymy does not appear to be justified.

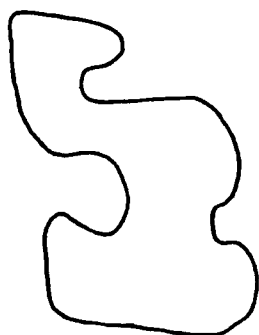


Figure 2.18c *Nerinella algarbiensis* Choffat.  
Fold pattern in single whorl section. BM(NH)  
GG22014. Aptian, Praia da Luz, Portugal.  
Actual whorl height = 3 mm. Actual whorl height  
= 3 mm.

## 2.26.2 *NERINELLA* species 1

(Figure 2.19a,b,c,d)

### Diagnosis

Extremely slender acicular shell with a very low apical angle. Whorl height is low relative to other *Nerinella* species. The labral fold is curved and points in an abapical direction.

### Material

BM(NH) GG22016 - GG22024

### Horizon and Locality

Lower Aptian (Bedoulian), Ericeira Port, Portugal.

### Description

Shell approaches cylindrical shape in later ontogeny. Very slightly concave whorl profile with a slightly raised narrow band around the suture. Two fine spiral striae composed of very finely knotted ornament occur 1/3 and 2/3 abapically down whorl walls. Internally the columella is slender. Whorl cross-section is quadratic; there are three simple internal folds (1,1,1,0).

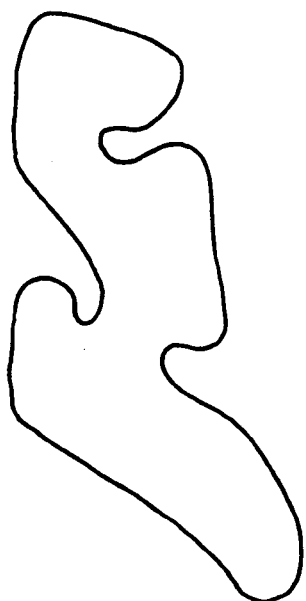


Figure 2.19d *Nerinella* species 1. Fold pattern in single whorl section. BM(NH) GG22020.

Lower Aptian, Ericeira Port, Portugal. Actual whorl height = 4 mm.



Figure 2.19a *Nerinella* species 1.  
External morphology. BM(NH)  
GG22018. Lower Aptian, Ericeira Port,  
Portugal.

Figure 2.19b External morphology (shell  
figured aperture uppermost as this shows  
ornament details more clearly). BM(NH)  
GG22019. Lower Aptian, Ericeira Port,  
Portugal.

Figure 2.19c Eroded shell segment  
showing extremely acicular shape.  
BM(NH) GG22017. Lower Aptian,  
Ericeira Port, Portugal.

### Occurrence

This species has been observed at only one locality at Ericeira Portugal (locality 61).

### Stratigraphic Range

*N. species 1* is found in the marno-calcaires à *Heteraster oblongus* which are Lower Bedoulian (Lower Aptian) in age (Rey, 1984).

### Discussion

The morphology of this species means its shells are unlikely to be well-preserved. The markedly acicular shape, which is extreme even for a *Nerinella* species, results in shells highly susceptible to breakage and also the loss of internal structure due to recrystallisation.

## 2.2.27 Genus *POLYPTYXISELLA* Pchelintsev, 1965

Type species. By original designation, *Nerinea clio* d'Orbigny, 1847.

### Diagnosis

"Narrow, elongate, turreted shells consisting of slightly concave whorls ... sutural ridge wanting ... without umbilicus. Aperture of rhombic outline, with five well-developed partly compound internal spiral folds. Range is Rauracian through Tithonian." Pchelintsev, 1968, p 38.

### 2.27.1 ?*POLYPTYXISELLA SCHICKI* (Fraas) 1867

(Figure 2.20a,b,c,d)

- p.1852 *Nerinea Syriaca* Conrad, plate 5 figures 35 and 37 only (? figure 33)
- \*1867 *Nerinea Schickii* Fraas, p 98, plate 4, figure 11
- 1878 *Nerinea Schickii* Fraas, p 242, plate 6, figure 1, ?plate 1 figure 11
- p.?1881-84*Nerinea Libanus* Quenstedt, plate 206, figures 28 and 29 only
- 1927 *Nerinea (Nerinella) Schicki* Frass; Blackenhorn, p 153 - 154, plate 8 (4), figures 60 - 62
- 1939 *Nerinella Schicki* Fraas: Delpey, p 158, text figures 116 and 117, plate 1, figures 2 - 4

#### Diagnosis

Whorls slightly concave with a slightly raised band around the suture, but flattening as shell size increases to become virtually flat when shell width is approximately 5 mm. Folds are simple and short except for the parietal fold which shows a slight tendency to bifurcate.

#### Material

BM(NH) G3809 (a large block containing numerous specimens).

Étallon Collection, Department des Sciences de la Terre, Université Claude Bernard, Lyon E19.12

#### Horizon and Locality

?Aptian, Deir-il-Kurkikfy, Lebanon (BM(NH) block). ? Kefraschona, Beyrouth (Lyon specimens).

### Description

Tapering extremely narrow conical shell which shows very regular growth. Early whorls bear fine nodules on the sutural ramp, and also a fairly coarse knotted spiral striae in the central part of the whorl wall. This ornament disappears as shell size increases - generally being completely absent when shell diameter reaches about 8 mm. A rather long canal terminates the aperture abapically. Whorl section is rectangular with five internal folds (2,1,2,0) and a slight basal swelling sometimes visible. The protoconch is heterostrophic (see Chapter 6 for a full description and discussion).

### Measurements

Apical angle: 13° (range 11° - 14°, N = 6)

### Occurrence

?*P. schicki* has been reported exclusively from the Middle East; Lebanon, Syria, Israel and Egypt (Blanckenhorn, 1927; Delpey, 1939).

### Stratigraphic Range

Only recorded from Aptian strata.

### Discussion

?*P. schicki* (Fraas) has been tentatively assigned to *Polyptyxisella* although the internal folds of ?*P. schicki* do not show the same degree of complexity as that shown in the type species (see d'Orbigny, 1852, plate 275, figure 5). In ?*P. schicki* only the parietal fold appear to show any sign of subdivision (Delpey, 1939, p 158, text figure 116) and this is not always apparent (see figure 2.20d). However in other respects ?*P. schicki* appears to conform to the *Polyptyxisella* diagnosis, although its stratigraphic occurrence is much later than the generic range given by Pchelintsev. There is, in any case, no doubt that the species belongs to the Nerinellidae.





Figure 2.20a *Polyptyxisella schicki* (Fraas). Three shells showing external morphology. All from the same large block BM(NH) G3809. ?Aptian, Deir-il-Kurkikfy, Lebanon.



Figure 2.20b Detail of left-hand specimen in figure 2.20a. Slit-band can be seen in abapical whorls.



Figure 2.20c ?*Polyptyxisella schicki* (Fraas). Detail of right-hand specimen in 2.20a. Rather pronounce abapical canal can be seen at the aperture.



Figure 2.20d External and internal morphology. Étallon Collection, Department des Sciences de la Terre, Université Claude Bernard, Lyon E19.12 Stratigraphic details unrecorded, ?Kefraschona, Beyrouth.



Conventional useage of the specific name "*schicki*" has been followed here. It is clear from Conrad's (1852) figures that some of the specimens included within "*N. Syriaca*" (plate 5, figures 35 and 37) belong to the same species as specimens referred to as *N. schicki* by later authors and herein. Other specimens figured by Conrad as "*N. syriaca*" (plate 5, figures 34 and 38) are now thought to belong to *D. cochleaeformis* (see section 2.17), and the remaining figures of "*N. syriaca*" (plate 5, figure 33, plate 11, figure 67 and plate 12, figure 72) are of uncertain affinities with regard to other described species. The original specimen of one of these latter figures has been located within the Yale University Museum Collection (Beecher, 1900), and this appears to be the only identified surviving specimen of the type series. The species *N. syriaca* Conrad, 1852 must therefore be based on this specimen which is a Nerineidae internal mould, probably belonging to *Eunerinea*. The species *N. syriaca* thus characterised bears little similarity to the specimens figured on plate 5 figures 35 and 37 (Conrad, 1852); these specimens are not therefore considered to form part of *N. syriaca*, but to belong to *N. schicki*, as described by Fraas (1867).

## 2.28 Genus **MULTIPTYXIS** Pchelintsev, 1953

Type species. By original designation, *Polyptyxis airigulensis* Fogdt (Pchelintsev, 1926, reported in Pchelintsev, 1968, p 38).

### Diagnosis

"Comparatively large, narrow, turreted, partially rod-shaped, multiwhorled shells with tubercles on the sutural ridge and a row of tubercles in the middle of the whorls. Obliquely tetragonal high aperture with five folds and the rudiment of a bottom fold. Range is Tithonian through Cenomanian" Pchelintsev, 1968, p 39.

## Discussion

This genus was erected by Pchelintsev (1953, reported in Pchelintsev, 1968). Pchelintsev (1968) incorporated *Multiptryxis* and *Triptyxis* Pchelintsev into the "family Triptyxisidae". The author considers that *Multiptryxis* belongs to the Nerinellidae on the basis of overall shell shape, and rejects the association with the rather conically shaped *Triptyxis*. *Multiptryxis* is therefore regarded as of uncertain subfamily placing.

Pchelintsev (1968, p 39) states that "*M. dolomieni* (Choffat) from the Vraconnian of Portugal ..... undoubtedly belongs to this genus" (ie *Multiptryxis*).

### **2.28.1 *MULTIPTYXIS DOLOMIEUI* (Choffat), 1901**

(Figure 2.21a,b,c,d)

\*1901 *Nerinella (Bactroptyxis) dolomiei* Choffat; Choffat, p 123, plate 5, figures 6 - 8

## Diagnosis

A gently concave whorl profile and a narrow sutural ridge bearing fine tubercular ornament. Whorl height is moderate.

## Material

BM(NH) GG22030 - GG22041

Geological Survey of Portugal Collection 1167 (no locality details recorded with specimen)

## Horizon and Locality

Albian, Praia do Sol, Ericeira, Portugal.

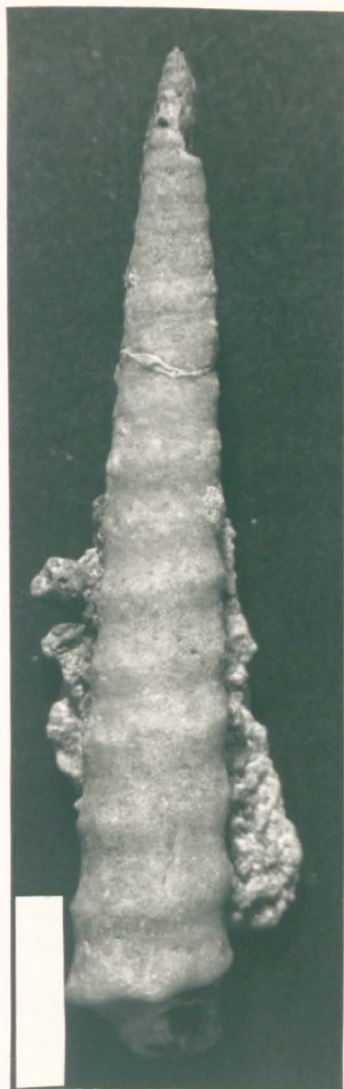


Figure 2.21a *Multiptyxis dolomieu* (Choffat).

External morphology. BM(NH) GG22040. Albian, Praia do Sol, Ericeira, Portugal.



Figure 2.21b Detail of external morphology.

BM(NH) GG22039. Albian, Praia do Sol, Ericeira, Portugal.

Figure 2.21c Eroded section showing internal folds.

BM(NH) GG22038. Albian, Praia do Sol, Ericeira, Portugal.

### Description

Very slender conical shells which show regular growth. Very fine spiral striae consisting of strings of small knots occur between the sutures. Internally there is a solid columella and a quadratic whorl cross-section showing five or six folds (3,1,1,?1) due to a slight basal swelling which is sometimes evident but does not form a significant fold. The abapical (ie lower) columella fold is large and shows bifurcation; the adapical columella fold is positioned in the columella/parietal corner, it is large and curved. The parietal fold is small and simple. The labral fold is medially placed, strong and shows slight bifurcation.



Figure 2.21d *Multiptyxis dolomieui* (Choffat).  
Fold pattern in single whorl section. BM(NH)  
GG22038. Albian, Praia do Sol, Ericeira,  
Portugal

### Measurements

Apical angle:  $12^{\circ}$  (range  $11^{\circ}$  -  $12^{\circ}$ , N = 6)

Sutural angle:  $105^{\circ}$  (range  $103^{\circ}$  -  $108^{\circ}$ , N = 4)

Whorl concavity index: 0.87 (range 0.86 - 0.87, N = 4)

### Occurrence

*M. dolomieui* has only been reported from Portugal (locality 69).

### Stratigraphic range

Albian.

## 2.29 GENUS 1

Type species. To be designated when published as G1 species 1.

### Diagnosis

Acicular tapering conical shell. Whorl profile rather flat; minimal or no ornamentation. Non-umbilicate; columella is slender. Whorl cross-section quadratic with four folds (1,1,1,1).

### Discussion

This genus is a typical member of the Nerinellidae, and is distinguished from other genera largely on the basis of fold pattern. The genus appears to be rare, and poorly diversified; the author has not encountered any species other than that described below.

### 2.29.1 G1 SPECIES 1

(Figure 2.22a,b,c,d)

### Diagnosis

Shell material is thin. Whorl profile is flat with no sutural ramps and shell exterior is smooth. The labral fold shows bifurcation at its end and the basal fold is small.

Material

BM(NH) GG21999 - GG22013 and GG22042

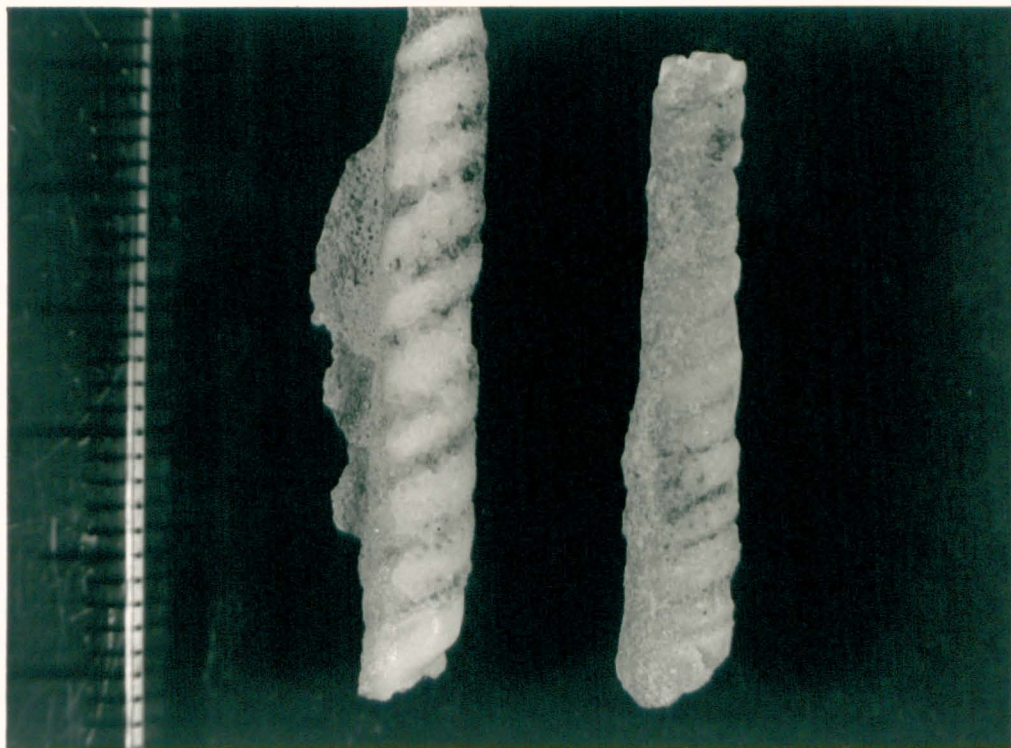


Figure 2.22a G1 species1. Internal moulds showing overall shell shape. BM(NH) GG22013. Lower Aptian, La Gabelle, France.



Figure 2.22b Eroded section showing overall shell shape and incomplete details of internal morphology. BM(NH) GG22006 (part of a large block). Lower Aptian, La Gabelle, France.

### Horizon and Locality

Lower Aptian (Bedoulian), La Gabelle, S of France.

### Description

Very slender tapering conical acicular shell. Internally there is a thin solid columella. The elongate quadratic whorl cross-section contains four folds (1,1,1,1).

### Measurements

Apical angle:  $9^{\circ}$  (range  $7^{\circ}$  -  $11^{\circ}$ , N = 10)

Sutural angle:  $113^{\circ}$  (range  $109^{\circ}$  -  $116^{\circ}$ , N = 12)

h/w ratio: 0.71 (N = 1)

### Occurrence

?G1 species 1 has been observed only in one area in southern France (locality 20, La Gabelle).

### Stratigraphic Range

At the above locality this species occurs in Bedoulian strata (Lower Aptian).



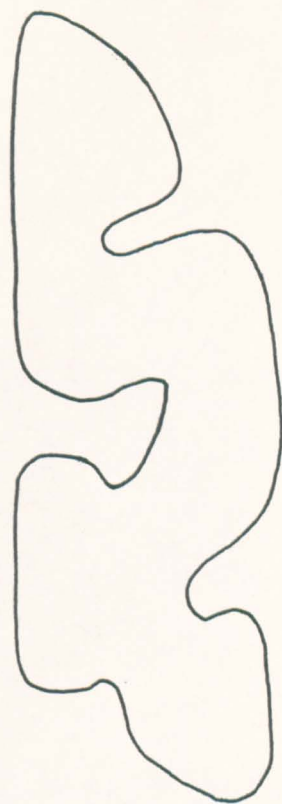
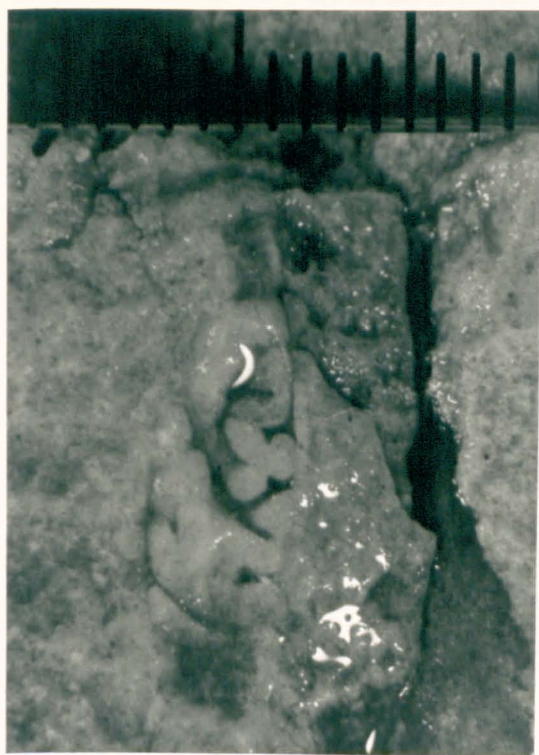


Figure 2.22c G1 species 1. Detail of fold structure in one whorl. BM(NH) GG22003. Lower Aptian, La Gabelle, France.

Figure 2.22d Fold pattern in single whorl section. BM(NH) GG22042. Lower Aptian, La Gabelle, France. Actual whorl height = 6 mm.

### Discussion

The fold pattern (1,1,1,1) of ?G1 species 1 is atypical of *Nerinella* (where a 1,1,1,0 pattern is characteristic). If consistency in nerineid taxonomy is to be maintained, this difference in fold structure, which appears to be quite unusual, should be considered to indicate a separate and new genus.

?G1 species 1 resembles *N. algarbiensis*, particularly in respect of its gross morphology, smooth shell and flat whorl profile. However, ?G1 species 1 has a slightly more cylindrical shell shape, and also differs internally with a bifurcating labral fold (simple in *N. algarbiensis*) and a basal fold (lacking in *N. algarbiensis*).



## CHAPTER 3

### INTRASPECIFIC MORPHOLOGICAL RANGE

#### 3.1 Introduction

In the Nerineacea, as in almost all living and fossil organisms, the practical separation of the group into basic biological units (ie species) is based on morphology. If two shells are sufficiently similar, the organisms are deemed to have belonged to the same species; in strict biological interpretation of "species" they could potentially interbreed to produce viable offspring<sup>1</sup>. If shells are significantly dissimilar they are considered to belong to different species.

Within extinct groups such as the Nerineacea, which disappeared towards the end of the Cretaceous, there are no extant related organisms which can be used to assess the degree of shape variation which should be accepted within a single species group. There is a heavy reliance on the "morpho-species" concept which is considered to reflect to some extent the boundaries of true biological species. The criteria used to separate one species from another are, by necessity, somewhat arbitrary, although palaeontologists usually favour criteria which show discontinuous variation between morpho-species.

Most nerineid "species" are based on a very restricted number of moderately or poorly preserved specimens often from a single or limited number of areas. In such cases it can be extremely difficult to decide how much variation should be allowed within a single "species", and also which characters show discontinuous variation appropriate for species level resolution.

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<sup>1</sup>"Species are groups of interbreeding natural populations that are reproductively isolated from other such groups" Mayr, 1963, p 12.

The occurrence of large numbers of well-preserved specimens can therefore provide a valuable opportunity for testing the continuous or discontinuous nature of various morphological features commonly used at species level in taxonomy.

### 3.2 Material

This study is based on material housed in the BM(NH) Collection under the numbers 83694, G17262 and G19451 which are labelled as "*N. gemmifera*" (more properly *Diozoptyx cochleiformis* - see section 2.17). Within these registration numbers there are a total of 54 specimens, 31 of which were measured for this investigation. Although the locality details recorded with the three specimen groups varies in detail<sup>1</sup>, the type of preservation and the associated sediments in all three cases are virtually identical. It seems likely that the specimens are all from the same locality or at least nearby sites. The morphological variation is, in any case, apparent within each of the three registered groups of specimens.

### 3.3 Approach

Preliminary examination of the specimens revealed that a wide range of overall shell shapes were grouped together within the same species. The specimens varied from regular isometric conical shells to those showing a pronounced cyrtconoid shape reflecting marked ontogenetic change in growth form. In figure 3.1, two shells

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<sup>1</sup>BM(NH) 83694:- Gazelle Hollow, Abeih, Lebanon. Cretaceous. R Damon Collection 1878. 6 specimens.

G17262:- Gazelle Hollow, Abeih, Lebanon. Cretaceous. C.H.V. Gollmer Collection. July 1896. 37 specimens.

G19451:- Gazelle Mountain, Lebanon, Syria. Cretaceous ?Turonian. Fahid Collection purchased Rev. C. Gollmer 1907. 11 specimens.

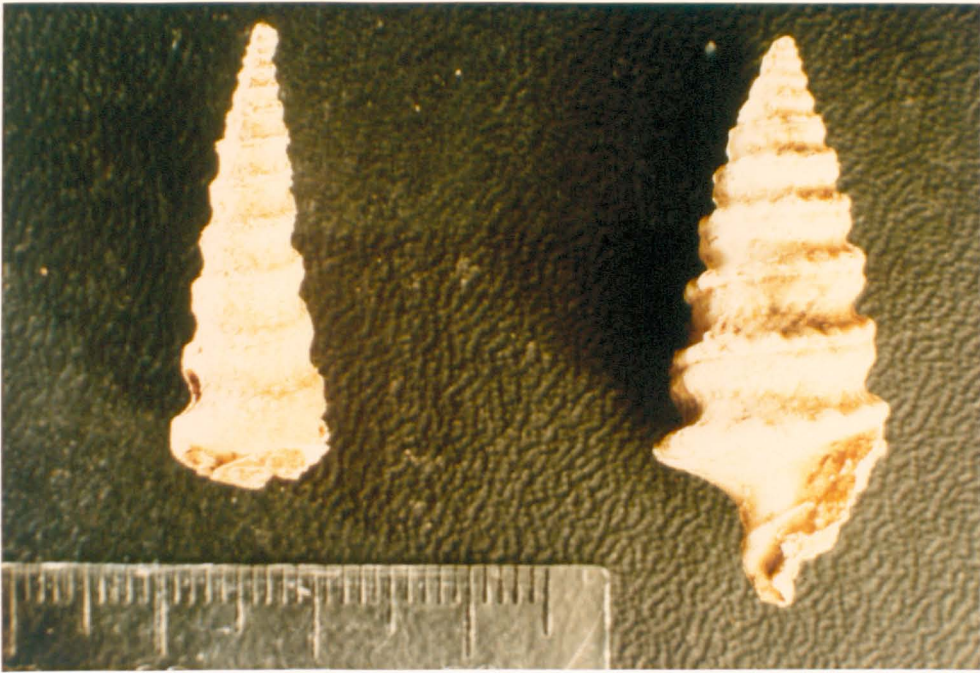


Figure 3.1 *Diozoptyx cochleaeformis* (Conrad). Two shells illustrating the "extremes" in morphology which are present. BM(NH) G17262. ? Turonian, Gazelle Hollow, Abeih, Lebanon.



Figure 3.2 *Diozoptyx cochleaeformis* (Conrad). Shells illustrating the range of intermediate forms connecting the two "extremes". BM(NH) G17262. ? Turonian, Gazelle Hollow, Abeih, Lebanon.

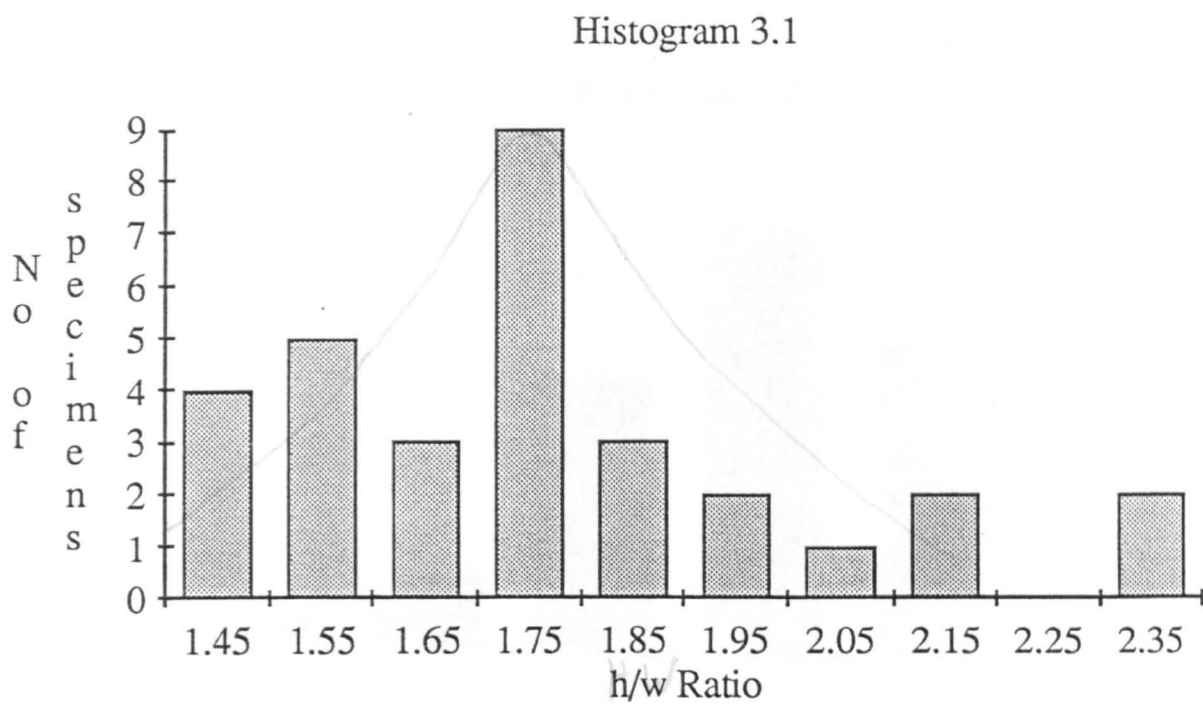
representing either "extreme" are figured side by side. There is a marked difference in overall shell shape and whorl concavity; if these two shells had been the only specimens available, the author would almost certainly have considered them to represent two different species. However, examination of all the specimens available clearly shows that the variation is not discontinuous, but that a complete spectrum of intermediate forms exists. This is shown in figure 3.2. A detailed analysis of this morphological range involved the measurement of whorl concavity index and overall H/W ratio, which is not comparable to whorl h/w ratio given in species descriptions in Chapter 2. This latter measurement was used because the nature of preservation had rendered the material extremely brittle and therefore unsuitable for sectioning. Measurement of h/w ratio per whorl would therefore have been difficult and the results of questionable accuracy. The H/W ratio reflects the overall shape and therefore growth form of the shell. It was considered to be the most direct and reliable way of quantifying shell form. The irregular growth pattern shown by some of the shells precluded the use of apical angle as a reliable indication of overall shell shape.

Both parameters were measured at approximately 15 mm shell height to minimise the effect of any ontogenetic variation.

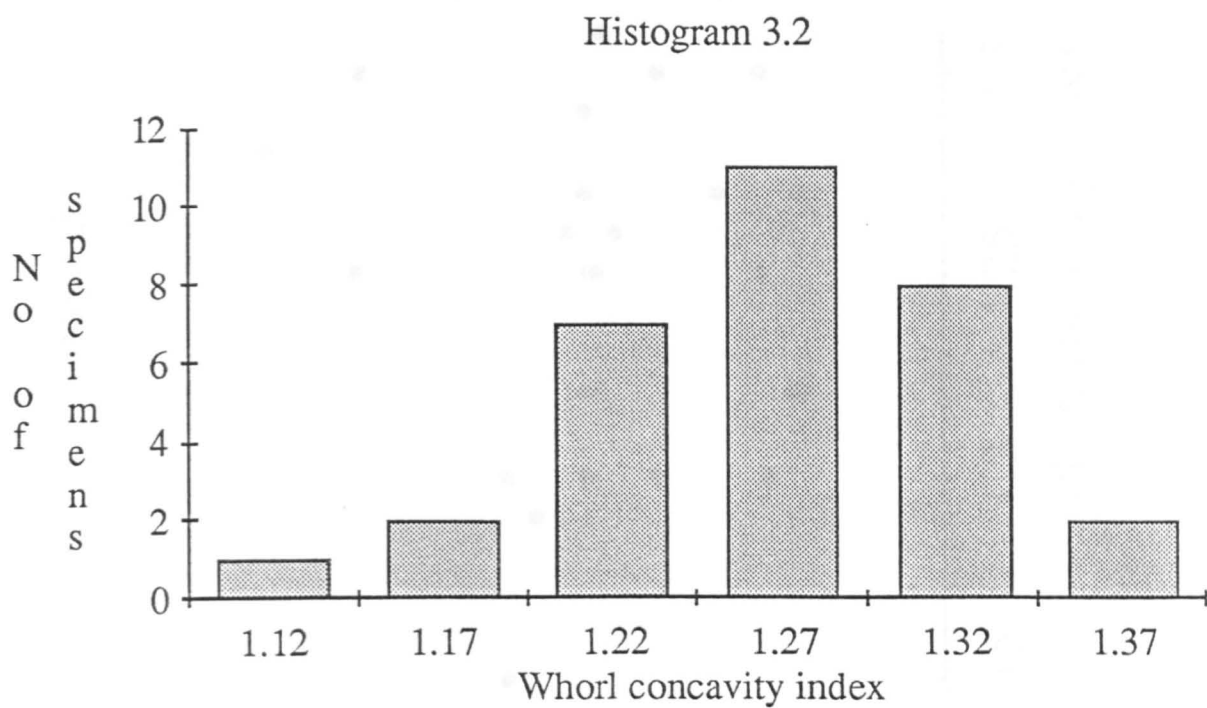
### 3.4 Results

The results are shown graphically in the scatter graph given in graph 3.1, from which it can be seen that a complete range of H/W ratios and whorl concavity indices exists (see Appendix 2 for primary data). Although a wide variation in values occurs, there are no distinct groupings which can be separated; intermediate forms completely link the extreme examples. In addition, no clear cut relationship exists between whorl concavity and H/W ratio.

The histograms 3.1 and 3.2 show the frequency distributions of H/W ratio and whorl concavity index separately. In the case of whorl concavity, an almost perfect normal distribution exists, which is entirely typical of a single discrete group. The situation is

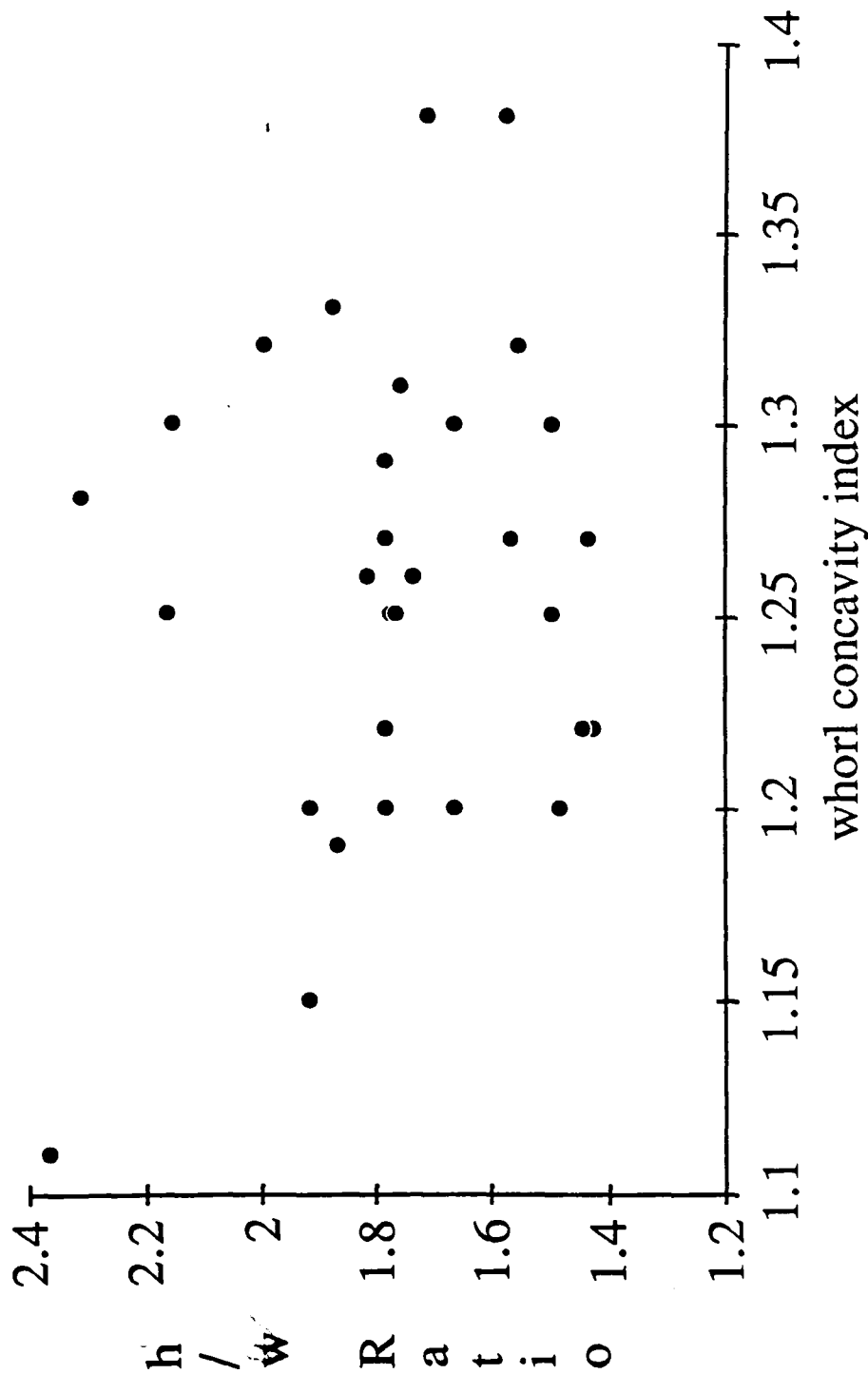


Histogram 3.1 H/W Ratio measurements in *D. cochleaeformis*.



Histogram 3.2 Whorl concavity index measurements in *D. cochleaeformis*.

Graph 3.1



Graph 3.1 Scattergraph of whorl concavity index against H/W ratio in *D. cochleaeformis*.

not so clear cut in the H/W ratio histogram (figure 3.1) where the distribution tends towards normal, but shows some variation from the ideal, for example, a slight positive skew at the lower end of the H/W ratio scale, and the isolated occurrence of specimens towards the upper end. This variation from a perfect normal distribution can be analysed statistically to determine whether or not it is significant (Krumbein and Graybill, 1965; Davis, 1973; Parker, 1979).

Firstly a "goodness-of-fit" ( $X^2$ ,  $\text{Chi}^2$ ) test can be used to test that the frequency distribution in the main part of the histogram does not depart significantly from a normal distribution. The formula:-

$$X^2 = \sum \frac{(O - E)^2}{E}$$

is used where O = observed frequencies and E = expected frequencies, which are obtained by superimposing a typical normal distribution curve on histogram 3.1. The values used are given in Table 3.1.

Class	Observed	Expected	Difference (O-E)
1.45	4	2	+2
1.55	5	4	+1
1.65	3	6	-3
1.75	9	9	0
1.85	3	6	-3
1.95	2	4	-2
2.05	1	2	-1
2.15	2	1	+1

TABLE 3.1



These figures give us:-

$$X^2 = \frac{4}{2} + \frac{1}{4} + \frac{9}{6} + \frac{9}{6} + \frac{4}{4} + \frac{1}{2} + 1$$

$$\text{therefore } X^2 = 7.75$$

The value of  $X^2$  can be looked up in statistical tables (Parker, 1979) under the appropriate degrees of freedom category. In this case there are 7 degrees of freedom, as the number of classes used (N) is 8, and degrees of freedom are usually taken to be equal to (N - 1). The  $X^2$  value at 7 degrees of freedom gives a probability between 0.1 and 0.5. This means that the variation between the actual and expected observations based on an expected normal distribution has between 10 to 50% probability of resulting from chance. Standard statistical procedure requires a chance probability of 5% or lower before any significance can be attached to the deviation. The difference between the observed and expected results is therefore not significant, and the actual distribution can be regarded as a sample from a normal distribution.

The anomalous "tail" of observations in the higher H/W classes can now be tested to determine whether or not it represents a significant departure from the normal distribution. Student's "t" test is used in this case because the total number of observations (ie sample size) is relatively small.

Firstly the sample mean is calculated:-

$n$  = number of measurements

$x$  = value of measurements

$\sum x$  = total value of measurements (frequency x measurements)

$$\text{Sample Mean } (\bar{x}) = \frac{\sum x}{n}$$

$$= \frac{54.75}{31}$$

$$\text{therefore } x = 1.77$$

Then standard deviation is calculated:-

$$\text{Standard deviation (s)} = \frac{\sum x^2 - \frac{(\sum x)^2}{n}}{(n - 1)}$$

$$= \frac{107.25 - \frac{(54.75)^2}{31}}{30}$$

$$\text{therefore } s = 0.593$$

To test whether the "anomalous" measurements at the upper end of the h/w ratio scale differ significantly from the rest of the sample, the statistic "t" is computed:-

$$t = \frac{\text{actual deviation}}{\text{standard deviation}}$$

$$= \frac{(2.35 - 1.77)}{0.593}$$

$$\text{therefore } t = 0.978$$

Where actual deviation = "anomalous" value - mean value

This value for t, at 30 (ie n - 1) degrees of freedom, gives, from Student's t table (Parker, 1979) a probability of approximately 20% that such "anomalous" measurements could occur at either end of the histogram due to chance. As, in this case, deviation in only one direction is being considered (a "one-tailed" test), this probability should be halved. The final probability of around 10% is well above the 5% probability limit used as a standard to isolate significant variation.

In summary, the variation shown is completely continuous, and there does not appear to be any relationship linking H/W ratio to whorl concavity index. The distributions of

parameters do not differ significantly from normal distribution patterns. This indicates that a single morphological group is present.

### 3.5 Discussion

Although considerable variation can be seen in the specimens of *D. cochleaeformis* studied, such variation is completely continuous. It is not possible to separate distinct morphological units, so it must be concluded that the variation occurs within a single morpho-species.

The morphological range present within this single nerineid species obviously has implications for species resolution within the whole superfamily, and also the characters which should be used to delineate species. In the case of *D. cochleaeformis*, variation in overall shell shape and the degree of whorl concavity was marked; conversely, external ornamentation appeared to be virtually constant as did internal fold structure, although in the latter case, the mode of preservation has tended to obliterate all traces of the original fold structure, so that this could be seen in only a few specimens.

It is not clear whether this study of *D. cochleaeformis* demonstrates the variation which would be typical of any nerineid species, or whether such variation is unusual and reflects the particular conditions (environmental, genetic or other) operating on these particular specimens. There is, unfortunately, no further information available concerning the collection and locality details other than that given above (R. J. Cleevely, pers comm) so it is not possible to conjecture any environmental or evolutionary influences which may have affected morphology.

This study has made use of material unique both in terms of the quality of external preservation and the number of specimens available. Certainly some other nerineid species appear to show considerable morphological range (see *Julesia pellati*, section 2.23.1 and *Pchelinsevia coquandiana*, section 2.18.2), but the material available has not enabled detailed analysis of the variation present. Conversely, other species appear to be extremely constant in overall morphology (eg *E. chloris* section 2.8.5).

The morphological range within the species *D. cochleaeformis* has caused much taxonomic confusion, with at least six "different" species erected and five varieties (Delpy, 1939) apparently based on the single group (see section 2.17 for further discussion of this point).

### 3.6 Conclusions

#### Specific

- 1 considerable variation in overall shell shape and whorl concavity exists within the material examined
- 2 this variation is continuous; it is not possible to separate the specimens into distinct groups
- 3 the specimens are therefore considered to belong to a single morpho-species which shows pronounced variability

#### General

- 4 whorl concavity and overall shell shape may vary considerably within a single nerineid species and should therefore not be used as the only criteria when distinguishing species
- 5 ornamentation and internal structure appear to be fairly constant within nerineid species
- 6 certain nerineid species (in particular *D. cochleaeformis*, *J. pellati* and *P. coquandiana*) show quite marked morphological variation, whereas in others (eg *E. chloris*) shell morphology is rather constant.

## CHAPTER 4

### PALAEOECOLOGY AND PALAEOBIOLOGY

"Although much of the general structure, decoration and sculpture of the gastropod shell appears to be wholly unrelated to the environment in which the animal lives, this is not entirely so ...." Fretter and Graham, 1962, p 76.

#### 4.1 INTRODUCTION

The Nerineacea is a large group, containing a wide diversity of morphologies; it is likely that they also showed a range of ecologies and habits. Some evidence of palaeobiological differences between different groups has been found, but it is likely that the overall picture is far from complete. The evidence and discussion given in this chapter inevitably reflects the author's main area of experience with the Nerineacea, the Lower Cretaceous forms. However, this includes a wide range of morphologies, which cover most, though not all, of the spectrum of form present within the group.

Shell morphology can only be related to function to a limited extent in living gastropods. In addition, snails show complex ecologies that cannot easily be categorised. The evidence available to palaeontologists is woefully small, and the scope for misinterpretation and disputation correspondingly great. The conclusions drawn in this chapter are therefore tentative "best guesses" based on the information available.

## 4.2 FUNCTIONAL MORPHOLOGY

In the absence of direct evidence, such as pre-mortal encrustation, various morphological criteria can be used to infer the probable mode of life of extinct snails. Functional analysis of gastropod shell form has been pioneered by Vermeij (1970, 1971, 1973, 1974), Linsley (1977, 1978 a and b), Palmer (1980) and Signor (1982 and 1984). This work has been based upon observations of the morphology and behaviour of living gastropods, which are then used to derive a number of predictions concerning the association of certain morphological traits with particular life habits. These predictions can be tested by applying them to extant groups where morphology and specific ecology is well known (Palmer, 1980; Signor, 1982); the predictions can also be applied to extinct snails to infer their probable mode of life (Linsley, 1978a; Signor, 1982). Of particular interest are the criteria developed by Signor (1982) to distinguish the mode of life of turritelliform gastropods.

In Table 4.1, Signor's criteria have been detailed alongside some of the major Nerineacea genera covered in this study. The final column gives the life mode indicated by the morphological parameters used. As the results show, there is conflicting evidence in almost all cases, so that only very tentative general conclusions can be drawn. The parameters used by Signor present some problems when applied to nerineid genera (see below), however, they highlight the morphological aspects which should be focused upon in a functional consideration.

### 4.2.1 Apertural Form

Signor (1982) followed Linsley's (1977) ideas concerning the implications which tangential apertures (where the plane of the aperture is tangential to the body whorl) or radial apertures (where the plane of the aperture passes through the axis of coiling) have for mode of life. However, Signor considered that, in high-spired forms, a "tangential" aperture should lie in the same plane as the ventral side of the shell; this was referred to as a displaced tangential aperture. It was noted that gastropods which

Table 4.1 Functional morphology analysis of various Cretaceous nerineid genera.

Genus	Apertural morphology	Columella fold	Shell sculpture	Whorl outline	Umbilicus	Disjunct coiling	Indicated life mode
<i>Eunerinea</i>	displaced tangential	Yes	minimal	concave	No	No	mobile epifaunal or possibly burrowing
<i>Pchelinsevia</i>	displaced tangential	Yes	minimal	concave or flat	Yes (wide)	No	mobile epifaunal
<i>Nerinella</i>	displaced tangential	Yes	minimal	flat or concave (rare)	No	No <sup>1</sup>	mobile epifaunal or burrowing
<i>Aphanoptyxis</i>	displaced tangential	No	minimal	flat or concave	Yes (narrow)	No	mobile epifaunal
<i>Diptyxis</i>	displaced tangential	Yes	minimal	flat or concave	No	No	mobile epifaunal

<sup>1</sup>See section 4.2.6

TABLE 4.1

grew continuously (as the Nerineacea apparently did - see Section 4.5) could only develop an approximation of a displaced tangential aperture, for example by having opisthocline or opisthocyrt apertures. Nerineid specimens with intact apertures are extremely rare; apertural morphology is usually inferred from growth lines and whorl morphology. All Nerineacea show opisthocline growth lines (Cossmann, 1898), so it may be deduced that all possessed opisthocline apertures which approximated to displaced tangential apertures. Signor (1982, p 380) states that "a displaced tangential aperture inhibits burrowing", and notes that sedentary and burrowing forms do not need displaced tangential apertures. Signor's own analysis of this parameter using extant species showed that 15% of burrowing forms had displaced tangential apertures although no sedentary species possessed them.

The apertural morphology of the Nerineacea seems to indicate a primarily epifaunal existence; however, the opisthocline growth lines are used to unify the group systematically. Nerineids may have had an opisthocline apertures simply because their ancestors did. These "ancestral features" could have been retained and would not necessarily reflect life modes. In addition, the opisthocline aperture may reflect the presence of a posterior slit terminating the aperture apically rather than relating to movement or behaviour.

#### 4.2.2 Columella Folds

Signor envisages a buttressing function for columella folds which is more necessary in burrowing, where much greater muscle exertion is necessary than in crawling. Burrowing forms are therefore more likely to have columella folds; in the analysis, only 3% of epifaunal forms have such folds as opposed to 93% of burrowing species (Signor, 1982). However, the precise nature of a "columella fold" is not defined and nerineid columella folds are somewhat different from those of other gastropods. This may indicate that the functional relationship between columella folds and a burrowing habit is not applicable in the case of nerineids (see Section 4.3).



#### 4.2.3 Shell Sculpture

This feature is not well-developed in any nerineid. Throughout the superfamily, ornament is restricted to rounded tubercles on the sutural ramps and finely knotted spiral striae between sutures. Such ornament would not affect burrowing activity but does not preclude an epifaunal existence.

#### 4.2.4 Whorl Outline

Signor (p 380) predicts that "actively burrowing snails should have a laterally flattened whorl cross-section" as this reduces the "projected area of the shell in the direction of movement". Most nerineids have either concave or flat whorl profiles which would be suitable, in energy terms, for burrowing. However, Signor also notes that rounded whorls tend to "entrain" sediment between the whorls resulting in increased mass and therefore a higher energy expenditure in burrowing. The nerineacean sutural ramps, which are common throughout the group, would presumably act in a similar way and would therefore demonstrate poor adaptation to a burrowing existence.

#### 4.2.5 Umbilicus

An umbilicus acts in two ways to preclude burrowing; firstly, it increases the shell area projecting perpendicular to the direction of movement, thus increasing the energy required (Signor, 1982); secondly if the umbilicus is open, it would tend to fill with sediment and increase shell mass, further raising the energy expenditure in burrowing. Within the Nerineacea, widely umbilicate genera often have abapical carinae which project into the umbilical space (eg *Pchelinsevia*, figure 4.1), these carinae would have reduced the area of the umbilicus open to the exterior, however, a space is usually still present through which sediment could have entered. It therefore seems highly unlikely that widely umbilicate genera were infaunal.



Figure 4.1 The wide, open umbilicus of *Pchelinsevia* species indicates that such forms were unsuited to a burrowing infaunal mode of life

#### 4.2.6 Disjunct or Open Coiling

Shells showing disjunct or open coiling can be regarded as reflecting a sedentary mode of life (Signor, 1982). Among the Nerineacea there are two reports of open coiling. Delpey (1939, p161) reports a new species "*Nerinella libanotica* Delpey" which shows open coiling in its later whorls. This species has a square whorl cross-section, which is atypical of the group, and does not possess any folds. Delpey, however describes a juxtasutural band and figures opisthocline growth lines, both of which indicate that the shell is nerineacean. *N. libanotica* was evidently a sedentary organism, at least during its later ontogeny. However, this is an isolated report of open coiling in the Nerineacea, and it should be emphasised that the other characters of the species are rather unusual. This evidence does not therefore indicate a sedentary mode of life for other nerineids.

Wieczorek (1979, p 316) states "some nerineaceans show a trend to uncoil the shell, demonstrated by the less close attachment of the last whorl to the penultimate one than in the case of any earlier whorl". An example is figured (Plate 8, figure 4) of a *Prygmatis bruntrutana* (Thurmann) specimen which shows that, despite a reduction in contact between the last whorl present and previous whorls, a regular conical shape is maintained; the last whorl remains joined to the previous whorls and follows the same coiling pattern as the rest of the shell. This does not, therefore, represent open or disjunct coiling.

#### 4.2.7 Analytical Conclusions

Gastropod behaviour patterns are not usually simple; almost all epifaunal forms associated with soft substrates (as the Nerineacea were) burrow periodically (Palmer, 1980; Signor, 1982). Conversely primarily burrowing forms commonly crawl epifaunally (Signor, 1982) and some cannot easily be classified as either infaunal or epifaunal (eg *Acteon tornatalis* Lamark, Section 4.7). It is therefore perhaps not surprising that the results of this functional analysis are not conclusive. However there is a general indication that most of the nerineid genera assessed were predominantly mobile epifaunal organisms, especially those with wide umbilici. This is supported by pre-mortal encrustation, which has been reported on both conical and more cylindrical nerineid shells (Section 4.5). The most doubtful epifaunal genus is *Nerinella*, which, with an extremely acicular streamlined shape and predominantly flat whorls, could have had a mainly infaunal existence. The apparent extreme sensitivity of *Nerinella* shells to current action (section 4.10.1) may have made an epifaunal mode of life difficult or impossible, particularly in moderate or high energy conditions. Barker (1976) concluded that nerinellids were probably infaunal, despite reporting pre-mortal encrustation of a *Nerinella* species.

There is little evidence to connect the Nerineacea as a whole with a sedentary mode of life, although this may have evolved in isolated instances. In addition, the

environmental distribution of the group does not indicate filter-feeding as one of the likely modes of nutrition.

Most nerineid genera were probably mobile epifaunal gastropods, although nerinellids were likely to have been predominantly infaunal.

### 4.3 INTERNAL MORPHOLOGY

The most striking aspect of the internal morphology of nerineids is the frequent occurrence of rounded projections of calcium carbonate which can extend from any of the four whorl walls into the central cavity. These projections are referred to as folds; they are somewhat different from the folds or plaits which occur in other gastropods.

Although columella folds are relatively common among gastropods, folds on the parietal, labral and basal walls, all of which occur in the Nerineacea, are extremely rare. Also, in nerineaceans, folds are not present at the aperture, whereas in virtually all other gastropods possessing folds, these are maximally developed at the aperture (Barker, 1976). The folds develop gradually between half a whorl ( $180^\circ$ ) and one and a half whorls ( $540^\circ$ ) behind the aperture (figure 2.2), with columella and parietal folds appearing first, labral folds arise slightly more adapically (Barker, 1976). The body whorl of the nerineid was virtually fold-free, with only minimal undulations in the whorl walls. Once the basic fold arrangement is established, it remains constant throughout most of the shell with only minor alterations, such as bifurcation or simplification of individual folds. Folds are then progressively lost towards the extreme apex of the shell when whorl size becomes extremely small (Barker, 1976; Wieczorek, 1979).



Figure 4.2 Internal morphology demonstrating progressive development of folds behind the aperture. *Ptygmatis bruntrutana* Thurmann.

Internal folds are extremely common in the Nerineacea although some groups do not possess folds (eg *Aphanoptyxis*, *Aptyxiella*, Ceritellidae). These groups occur throughout the superfamily and cover the whole spectrum of shell morphologies present within the group. In addition, these genera do not show any ecological restriction; they occur in a variety of environments, often alongside other nerineids which possess folds.

Based on analogy with extant gastropods, the folds were formed behind the mantle cavity in an area of the shell occupied largely by the digestive gland, reproductive organs and, in the case of some opisthobranchs (Fretter and Graham, 1954), a pallial caecum.

The nature of the fold pattern, or the total absence of folds, is an important feature of a nerineid specimen. The internal position of folds means that they have a higher preservation potential than external shell features such as ornament. The constancy of fold pattern during ontogeny enables its use as a generic character (usually the overall pattern) and sometimes for species distinction (generally based on slight shape or position variation). Folds are therefore extremely important in nerineid taxonomy. However, the functional use of folds in the living nerineid is somewhat problematic. Fold number varies from zero to nine or ten, in different genera, and there appear to be no ecological differences between groups with widely differing fold number and complexity. Obviously some nerineids survived successfully without any internal folds; also the folds either did not serve a function at all within the body whorl of the shell, or did not serve a function valuable enough to sacrifice space within the body whorl.

Signor and Kat (1984, p 214) have suggested that the "complex pattern of internal spiral features that characterizes the Nerineidae" acted to prevent the insertion of crab chelae into the aperture prior to a "peeling" attack by the crab. The absence of folds at the aperture clearly precludes such a function, although folds may have been used for protection in a rather different way. The penultimate whorl of *Campanile symbolicum* is greatly thickened as an anti-peeling adaptation which is successful because the animal can retract deeply into the mid-whorls of its shell.(Houbrick, 1981). It is conceivable that in the Nerineacea the presence of folds within  $1\frac{1}{2}$  whorls of the aperture would have prevented any predatory peeling beyond this point, although the presence of the folds may have limited the depth to which the nerineid animal could retract into its shell.

The presence of folds would make a successful predatory attack on the shell spire more difficult in two ways; firstly a mid-whorl crushing attack (more likely than an attack at the suture because of the sutural ramps) would meet with high structural strength; secondly, even if the shell was broken, the extraction of soft tissue would be

difficult (Signor and Kat, 1984). Balanced against the possible functioning of folds as anti-predatory devices is the fact that the author has neither observed any signs of repair consistent with predator damage on any nerineid shell, nor seen any report of such evidence. In addition, it seems that shell breaking predation was relatively rare prior to Late Cretaceous/Early Tertiary times (Vermeij, 1983; Taylor, 1981); nerineids with folds first appeared in the Early Jurassic. Arguments for a defensive function of nerineid folds are therefore unsatisfactory, although a general strengthening function is plausible. Both *Turritella* and *Campanile* show secondary thickening within the shell spire which has been related to the need for increased shell strength (Wrigley, 1940 (*Campanile*); Andrews, 1974). In addition, such internal deposits affect physical properties such as the centre of gravity and density of the shell. Such secondary deposition is particularly common in high-spined gastropods for example Terebridae, Cerithidae, Vermetidae (Fretter and Graham, 1962; Vermeij, 1970) and has been related to the need to counteract buoyancy in empty whorls which have been abandoned by the snail. Such a function would be important in burrowing turritellids and terebrids, but would also be required by shell draggers such as the Campanilidae and high-spined Nerineacea (see Section 4.7).

Barker (1976) has suggested that the folds represented a method of eliminating excess calcium carbonate, which had been taken in during deposit feeding, from body tissue. If extra shell material had been precipitated on the shell exterior, this would have affected the mobility of forms envisaged to be infaunal such as *Bactroptyxis* (Barker, 1976). However, there appears to be little evidence that marine gastropods need to dispose of excess calcium carbonate by producing extra shell material (N. J. Morris, pers comm). Secondary deposition of calcium carbonate inside the shell is not a noted feature of infaunal deposit feeders living in carbonate environments today, also nerineids living in non-carbonate situations (including some of the earliest forms eg *Nerinella cingenda* from the Aalenian at Blea Wyke Nab, Yorkshire) still possess folds. In addition there does not appear to be any evidence of greater fold deposition

in nerineids inhabiting carbonate environments compared to those living in non-carbonate ones.

Fretter and Graham (1962) have suggested that in some instances where multiple columella folds are present, this reflects secretion from a mantle which has become folded because it is too large. Signor (1984) notes that such folds would be expected to have a random distribution, and to be maximally developed behind the aperture, reflecting the position of the body in a retracted state. The latter criterion is certainly fulfilled by the Nerineacea, but not the former; nerineids usually have only one or, more rarely, two columella folds, and the positioning of these is extremely constant within genera.

It has been suggested (Taylor, Morris and Taylor, 1980 citing Fretter and Graham, 1962) that the folds of the nerineid could have supported a "channelled ciliated mantle" (p 385) similar to the mantle caecum present in some opisthobranchs (eg Acteonidae), which appears to be involved in respiration, providing a respiratory surface and also access to the most apical parts of the visceral hump (Fretter and Graham, 1954). In lower opisthobranchs, ridges tend to develop on the right-hand side of the body, generating an exhalent current, and a pallial tentacle sometimes develops to form an exhalent siphon; the appearance of such ridges may be related to a reduction of mantle cavity depth which reduces the internal space available for the gill (Fretter and Graham, 1962). It is difficult to assess the likelihood of such a suggestion; it seems that extant opisthobranchs do not require support for their caecum, and that nerineids must have possessed a much larger (by an order of magnitude) and more divided structure if all the folds had this function.

Columella folds occur in many gastropod groups and are usually considered to provide extra surface area for the attachment of the columella muscle (Fretter and Graham, 1962). This suggestion has been criticised by Signor and Kat (1984) on the basis that columella folds at the aperture (as they occur in virtually all non-nerineid gastropods) would have been formed in anticipation of their later function, an



unnecessary step since the animal could secrete a fold behind the aperture when it was required for muscle attachment; the non-essential early development of a columella fold would also take up space in the body whorl. Signor and Kat's work on turritelliform gastropods has shown that, in the groups studied, the columella muscle attaches to the columella between  $2\frac{1}{2}$  -  $4\frac{1}{2}$  whorls behind the aperture. They have found that the muscle attaches to the columella on either side of the folds. The function of the folds therefore appears to be to buttress the muscle during contraction, confining the muscle to the area on the columella around the fold. Such support for the columella muscle is much more necessary in burrowing forms than in epifaunal shell draggers.

The implications of these results for the function of columella folds in the Nerineacea are not clear cut. Although nerineid folds appear behind the aperture, they would still be formed rather too early to represent muscle attachment sites, if the positioning of muscle insertion in extant high-spired gastropods is accepted as a model for the nerineids. On the other hand, if the columella folds had a buttressing function, the effect of this would be lost in the body whorl, and the overall efficiency of muscle action reduced.

#### 4.3.1 Conclusions

The regularity and constancy of the internal folds within species and genera might imply a particular, rather than general function, and in this respect, support for a series of delicate ciliated channels is perhaps the most attractive hypothesis. However, folds were not essential to nerineids and there appears to be little connection between fold number or complexity and either overall shell form or ecology. The folds may have had a more general function in controlling the centre of gravity of the shell and increasing overall shell strength in relation to environmental, rather than predation, pressures. The columella fold or folds may have acted to buttress the columella muscle when it contracted, although the effectiveness of this action would have been less in the Nerineacea than in other gastropods; the presence

of columella folds in the group probably does not therefore indicate a burrowing habit, as it does in other high-spired snails.

#### 4.4 APERTURAL MORPHOLOGY

The nerineid aperture is characterised by a short canal at the abapical anterior end, and a slit in an adapical posterior position, adjacent to the suture.

The abapical canal is likely to have contained some soft tissue extension, most probably, by analogy with extant gastropods, an inhalent siphon (Fretter and Graham, 1962), although discontinuities in the apertural margin are not exclusively related to water flow; for example the abapical notch in the Strombidae houses the snail's right eyestalk (Hickman, 1985).

The posterior slit probably represented the site of exhalent water flow; slits and sinuses in this position are usually interpreted as "hygienic" devices which enable better separation of inhalent and exhalent flow (Fretter and Graham, 1962; Knight et al, 1960). The positioning of the slit strongly indicates the asymmetric nature of the nerineid animal, with a single anterior gill and a posterior anus (Barker, 1976; Djalilov, 1979).

The opisthocline form of the aperture renders it of "displaced tangential" type, characteristic of non-burrowing forms (Signor, 1982, see Section 4.2.1).

#### 4.5 GROWTH

The growth lines which are occasionally visible on exceptionally well-preserved nerineid specimens are regular and uniform, indicating fairly constant and continuous growth throughout ontogeny. Nerineacean shells do not show varices, which would reflect prolonged growth halts, neither is there any evidence of apertural elaboration

which, in some groups such as the Cerithiidae and Potamididae reflects the termination of spiral shell development (Signor, 1982). In addition, some nerineid shells reached a considerable size. Incomplete specimens of *Eunerinea chloris* (BM(NH) 21254) are around 600 mm in length, and *Pchelinsevia toucasiaephila* has been observed insitu (locality 48) to reach lengths of 220 mm, which, with the widely umbilicate conical shell of this species, gives a rather massive gastropod. These sizes are not atypically large, in many nerineid groups, sizeable specimens occur, and there is no evidence of specimens reaching a "maximum" size.

It is concluded that nerineids had a fairly regular growth rate; they do not seem to have had a terminal or mature stage where growth stopped but appear to have grown continuously throughout ontogeny.

As the Nerineacea lived exclusively in tropical and subtropical seas, it is likely that both growth rates and calcification index were high (Graus, 1974; Wieczorek, 1979; Kohn, 1985).

#### 4.6 EPIZOANS

Encrustation and boring of nerineid shells are relatively common phenomena in many genera (eg *Eunerinea*, *Aphanoptyxis*, *Pchelinsevia*). The palaeoecological information which can be deduced from these epibionts is restricted to cases where there is clear evidence that the relationship developed during the life of the nerineid, for example where subsequent shell growth has enveloped the epizoan. The current study has not found any such unequivocal evidence for pre-mortal colonisation, but there are several reported examples of pre-mortal encrustations of nerineid shells.

Delpey (1938) describes a specimen, possibly *Nerinea salinensis* d'Orbigny, which has been completely encrusted by "*Milleporidium*". It is evident that this encrustation commenced during the life of the snail because the last whorl (where the original shell

structure is preserved) has enveloped some layers of the epibiont. The relationship between the two organisms is described as symbiotic, although the mutual benefits are not stated; these would probably have been a suitable substrate for the hydrozoan to colonise together with improved feeding opportunities; the nerineid would have gained protection by camouflage. Delpey reports that the "*Milleporidium* " had grown all over the shell, but that it is more thick on one side than the other; however she seems to be confused as to the implications of these observations, stating on p 354:-

"Il (ie "*Milleporidium*") est plus épais sur tout un côté de la Nérinée, plus mince sur le côté opposé que était sans doute inférieur quand l'animal traînait sa coquille" (It is thicker on one side of the nerineid, thinner on the opposite side which was, without doubt, underneath when the animal dragged its shell)

whereas on p 355:-

"C'est la position de la coquille dans l'espace qui paraît être cause de l'épaisseur moindre du *Milleporidium* sur un côté de la coquille. Le fait qu'il existe exclut l'hypothèse de la traction de la coquille vivante sur le sol" (It is the position of the shell in space which was apparently the cause of the reduced thickness of "*Milleporidium* " on one side of the shell . The fact that it exists excludes the hypothesis of movement of the shell living on the substrate)

It seems unlikely, however, that any behaviour exhibited by the gastropod would result in uneven distribution of the hydrozoan. Nerineids appear to have grown steadily (ie at the same rate) throughout life (see Section 4.5). The shell must have been first colonised while the gastropod was alive; this indicates that the snail was epifaunal. If the animal was sessile or sedentary, the growth of one whorl would have turned the shell through 360° if the animal was to avoid having its head/foot complex pressed into the substrate. This continuous revolution would have allowed the hydrozoan to colonise the shell evenly. Conversely, if the nerineid had been mobile, the shell may have been supported by the foot during locomotion (the species

is rather conically shaped - see Section 4.7) in which case no abrasion would have occurred (Palmer and Hancock, 1973). Even if the shell had been dragged, the side of the shell moving along the substrate would have been constantly changing as shell growth occurred, so that the effect of this abrasion would be approximately equal on all sides. The animal grew at least one whorl after the initial colonisation, but then died. There is no reason why the epibiont should have stopped growing when the gastropod died; it is highly likely that the uneven distribution of the colony resulted from continued growth on a now dead shell, which remained in a constant position in relation to the substrate, thereby inhibiting "*Milleporidium*" development on its lower surface.

Vogel (1968) reports the encrustation of a "*Nerinea*" by a rudist, *Sauvagesia*, which shows spiral growth of about 225° around the nerineid shell in the opposite direction to the growth of the snail. Vogel considered that the growth pattern shown by the rudist indicates that the attachment of the bivalve took place during the lifetime of the gastropod. He argues that this encrustation shows the "*Nerinea*" lived epifaunally, and that the heavy nerineid shell, together with the additional burden of the rudist would preclude rapid movement of the snail; from this he deduces that the snail was a filter-feeder, as it was not capable of the movement necessary for predation or grazing. The nerineid is not named, described or figured in any way that might indicate its taxonomic affinities. The relative sizes of the two organisms are not specified and the drawn figures (Vogel, 1968, figures 1a and b) which supposedly show the relationship between the two shells are extremely unclear.

The description which is given of the association could be explained, as Vogel suggests, by pre-mortal encrustation of a sedentary shell, with the rudist's development adjusting to a slow revolution of the gastropod shell as the latter grew; however it could equally well result from post-mortal disturbance of the shell. If the rudist had settled on one side of the shell, a disturbance or series of disturbances which resulted in a revolution of around 90° of the gastropod could have caused the

spiral development of the bivalve. It is conceivable that the weight of the rudist itself affected the stability of the gastropod shell, resulting in rotational movement. Vogel's assumption that the rudist encrusted a living gastropod is not proven; his statements concerning the living and feeding habits of the "*Nerinea*" cannot therefore be accepted as more than possibilities. It is unfortunate that his suggestions have been treated as facts (Dauwalder and Remane, 1979).

Barker (1976) reports several instances of pre-mortal encrustations and borings of nerineid shells:-

*Nerinella cf multistriata* - algal borings enclosed by succeeding whorl

*Melaniptyxis altaris* - oysters and serpulids where encrustations have been enveloped by later shell material

which, he concludes, implies an at least partially epifaunal existence for these species.

Pre-mortal serpulid encrustation of *Cryptoplocus depressus*, where the later shell whorl has covered the worm tube, is reported by Wiczorek (1979, plate 4, figure 5).

In conclusion, there is some evidence from pre-mortal epibiont colonisation of shells which is strongly suggestive of an epifaunal existence for some nerineids. However, inferences based on encrusted material which concern locomotion and feeding habits are not well substantiated.

#### 4.7 MOVEMENT

A wide variety of overall morphologies are included within the Nerineacea, and it is likely that different forms showed different behaviour and ecologies. However, some general inferences concerning the movement of major morphological groups can be made.

Many nerineids are high-spined, some extremely so (eg *Nerinella*, *Eunerinea*); even more conically shaped genera such as *Diozoptyx* and *Pchelinsevia* are high spined

compared to the overall spectrum of gastropod form. High-spined shells are usually dragged along the substrate surface as the energy required to lift the shell is excessive (Linsley, 1978; Signor, 1984, Kohn, 1985) eg some Terebridae (Hickman, 1985), Campanilidae (Wrigley, 1940). It is unfortunate that the continuous growth of nerineids (Section 4.5) means that no trace of shell dragging is likely to be left on fossilised shells as the area of the shell in contact with the substrate would have been continually changing as helical growth proceeded.

Given that some nerineid genera were epifaunal (Section 4.2 and 4.6) it is highly likely that high spined mobile nerineids moved their shell by dragging it behind them, at least in the later stages of ontogeny. Signor (1984) reports that shell draggers advance by extending the foot, then contracting the columella muscle (while the foot is stationary) so that the shell is drawn forward. The length that the shell can be moved in each contraction is proportional to the relaxed length of the columella muscle. It is therefore inferred that high-spined shells tend to have deeply inserted columella muscles which allow both efficient movement and deep retraction (Signor, 1984). The possible role of columella folds in muscle action is discussed in Section 4.3.

Linsley (1978) stated that shell draggers were amongst the very slowest gastropods, however, his conclusions have been severely criticised by Palmer (1980) who argues that drag has little effect on the energy used by a mobile gastropod; Palmer's research has shown that other factors such as the type of locomotion used and substrate type are much more significant.

More ovate shells such as *Phaneroptyxis* and *Itieria* could have supported their shell above the foot, as is seen in *Acteon tornatalis*, which has a shell form similar to *Itieria*. Field and laboratory observations of *A. tornatalis* have shown that this species "ploughs" along at the substrate surface, leaving characteristic deep furrows (figure 4.3) and also burrows, entering the sediment at about 50° (figure 4.4). It is unlikely, however, that *Itieria* burrowed, as it has a wide and rather open umbilicus (Section 4.2.5).

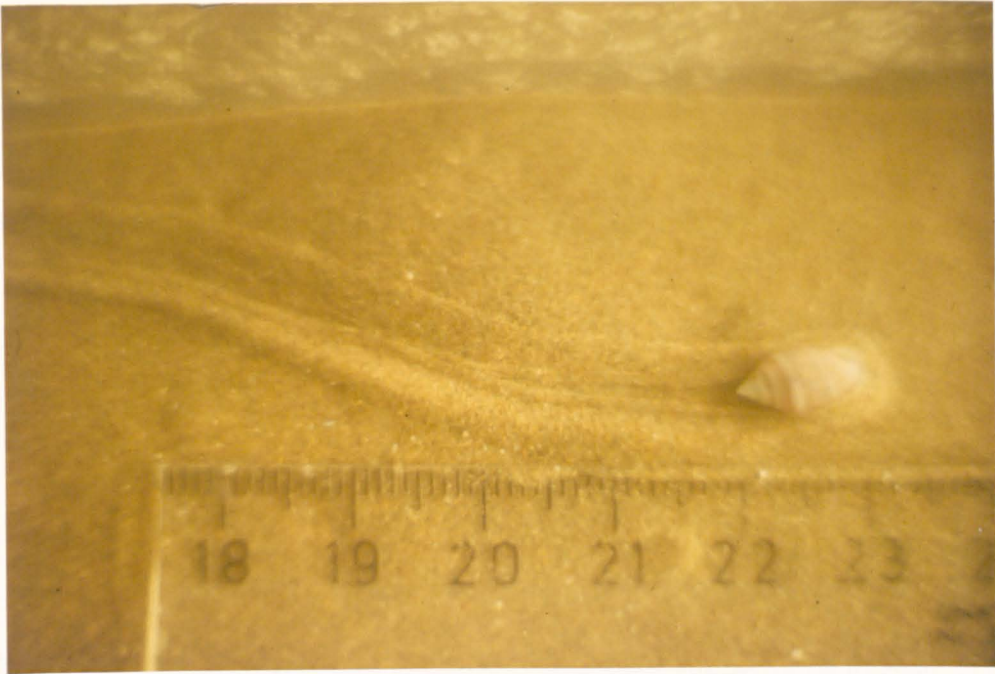


Figure 4.3 The characteristic furrows left by *Acteon tornatalis* as it moves across a sandy surface. *Itieria* species may have shown similar movement.



Figure 4.4 *A. tornatalis* burrowing into sediment (Itieria species probably did not burrow). The complex behaviour of this species, like many other gastropods, makes it difficult to classify them as either "epifaunal" or "infaunal".



#### 4.8 FEEDING

Shell form cannot be related to mode of nutrition, for example, if extant gastropods which are similar morphologically to some major nerineid groups are reviewed:-

*Terebridae* - predatory (Taylor et al, 1980)

shelled opisthobranchs - predators or herbivores (Taylor et al. 1980)

*Turritella* - ciliary filter feeder (Andrews, 1974)

*Campanile* - algal grazer (Houbrick, 1981)

the feeding habits which they show covers virtually the whole spectrum found within the Gastropoda. Comparison with extant forms does not therefore provide any direct evidence concerning the nutrition of the nerineids. Any suggestions must be based on inferences from indirect evidence. Such suggestions must, by necessity, be rather tentative and it is therefore highly unlikely that it will be possible to draw any firm conclusions concerning the predominant feeding mode of the superfamily.

Of the broad categories available, predation is perhaps the least likely. The Nerineacea have not been linked with predation by any worker; perhaps the common shell forms of the group (elongate, large, heavy) have instinctively been interpreted to indicate lack of speed which has implied poor predatory potential. Shell form is not strictly related to speed, however (Palmer, 1980) and predation does not always require fast movement.

Filter feeding has been proposed (Vogel, 1968, see section 4.6 for discussion) although the occurrence of nerineids in situations where there was considerable terrigenous influx (Section 4.10.2) indicates that such a mode of feeding was unlikely.

A herbivorous feeding habit has been proposed for the Nerineacea by Barker (1976) and Taylor et al (1980). Barker argued that the relative loss of digestive gland tissue caused by the presence of internal folds (estimated to reduce internal space by up to

56% in complexly folded *Bactroptyxis* species) indicated that food storage capacity within the nerineacean organism was severely limited. This would imply that nerineids, being unable to build up food reserves, must have had access to a reasonably constant food supply and were therefore herbivorous. However, nerineids may have elongated their digestive gland adaptically to make up for the loss of tissue caused by the internal folds (on average 25 - 30% for common Cretaceous genera, based on Barker's figures); alternatively a near continuous food supply could have been maintained by feeding on sessile organisms, provided that the prey was relatively abundant. Barker also notes that the dense concentrations of individuals showing no evidence of transportation indicates herbivorous habits. Unfortunately, in Cretaceous strata there is little evidence of untransported assemblages which show high population densities.

M. P. Watkinson (pers comm) has found that the development of algal mats in shallow water environments of Lower/Middle Jurassic age in Portugal is negatively correlated with the presence of nerineids. The mats tend to disappear from the fossil record when nerineids occur.

Despite the inconclusive nature of the evidence available, a herbivorous habit seems to have been the most likely feeding mode of the Nerineacea, although it is possible that the nerineids followed a range of feeding methods as is the case in many extant gastropod groups.

#### 4.9 PALAEOENVIRONMENTS

Nerineids are most commonly associated with carbonate facies of various types. There are many examples, particularly from the Upper Jurassic and Lower Cretaceous which illustrate this association; the Oxfordian/Kimmeridgian of Poland (Wieczorek, 1979), the Barremian/Aptian of Russia and France (Chernov and Yanin, 1979; Masse and Philip, 1981), the Aptian/Albian of the Americas (Allison, 1955;

Matthews, 1956) and the Albian/Cenomanian of Italy and Israel (Carbone, Praturlon and Sirna, 1971; Bein, 1976). This association has also been found during the present study at many Lower to Mid Cretaceous localities in France and Portugal (localities 7, 17, 18, 25, 34, 45, 46, 46a, 48, 59, 60).

Nerineids which occur in such sediments tend to show quite wide generic diversity (eg *Eunerinea*, *Pchelinsevia*, *Prygmatis*, *Favria*, *Diptyxis*, *Phaneroptyxis*, and more rarely, *Nerinella*<sup>1</sup>) and are associated with rudists, corals, echinoids, stromatoporoids and other bivalves such as limids and *Neithea*. The sediments involved include wackestones, packstones and grainstones, reflecting a concomitant variety of energy levels. Major facies such as the urgonian limestones of southern France are thought to have formed on off-shore highs, remote from any sources of terrigenous material (Masse and Philip, 1981). In general, an environment of clear, shallow warm water of normal salinity is indicated, with a variety of energy levels. The sediments are associated with offshore shallowing reflecting a biohermal or biostromal build-up which was usually based on rudists and corals (Masse and Philip, 1981; Rey, 1979). Nerineids appear to have inhabited both the high energy environments on the build-up itself, where water depth was shallow, and also areas around the build-up where depth was greater and energy levels lower. In very high energy environments the nerineids which occur are large and thick shelled (*Eunerinea*, *Pchelinsevia*), for example, frequent whole specimens of *P. toucasiaephila* (Dietrich) occur in coarse cross-bedded grainstones of Lower Aptian age at Crismina Fort (locality 48), Portugal.

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<sup>1</sup> Although *Nerinella* species are relatively less common in such facies, this may not reflect a true difference in original distribution - the morphology of the *Nerinella* shell means that it is more likely to be broken up prior to burial, and also to be lost by taphonomic processes (see p 122).

In general nerineid diversity was high in such areas, at least during the Upper Jurassic and Lower Cretaceous, however the situation appears to have changed in the Upper Cretaceous, when, alongside a change in build-up character from mixed coral-rudist associations to rudist-dominated ones (Rey, 1979), the surviving nerineid genera appear to have lived mainly outside the build-up area, as is seen in the distributions patterns and associated fauna within the Gosau deposits (see below).

Occasionally dense mono-generic or mono-specific nerineid beds occur which contain few other macrofossils for example at Lagarde d'Apt, France (locality 34) where *Phaneroptyxis* specimens are closely packed (figure 4.5) with only a few isolated rudists present. In this exposure, the nerineids do not show evidence of significant transport, the shells, although admittedly not delicate, appear to be extremely well-preserved, a wide size range is present and there is no preferred orientation. The sediment is extremely pure chalky limestone, indicating that these nerineids were living in a low energy environment probably at moderate water depth in conditions of slow sedimentation which enabled the shells to accumulate in such high densities. Similar developments are reported from the Upper Jurassic (Wieczorek, 1979; Dauwalder and Remane, 1979) but are rather less common in the Lower Cretaceous, where, in most instances of nerineid shell beds there is clear evidence of allochthonous origin. Such high concentrations of apparently insitu nerineids have been used as evidence that the Nerineacea were herbivores (Barker, 1976; section 4.8).

#### 4.9.1 Non-Carbonate Associations

Nerineids were not, however, restricted to carbonate dominated environments; there are several associations which indicate that some nerineid genera were tolerant of more restricted conditions, at least by the Lower Cretaceous; in the Upper Jurassic, nerineids do not appear to occur in marly or shaly facies (Wieczorek, 1979).

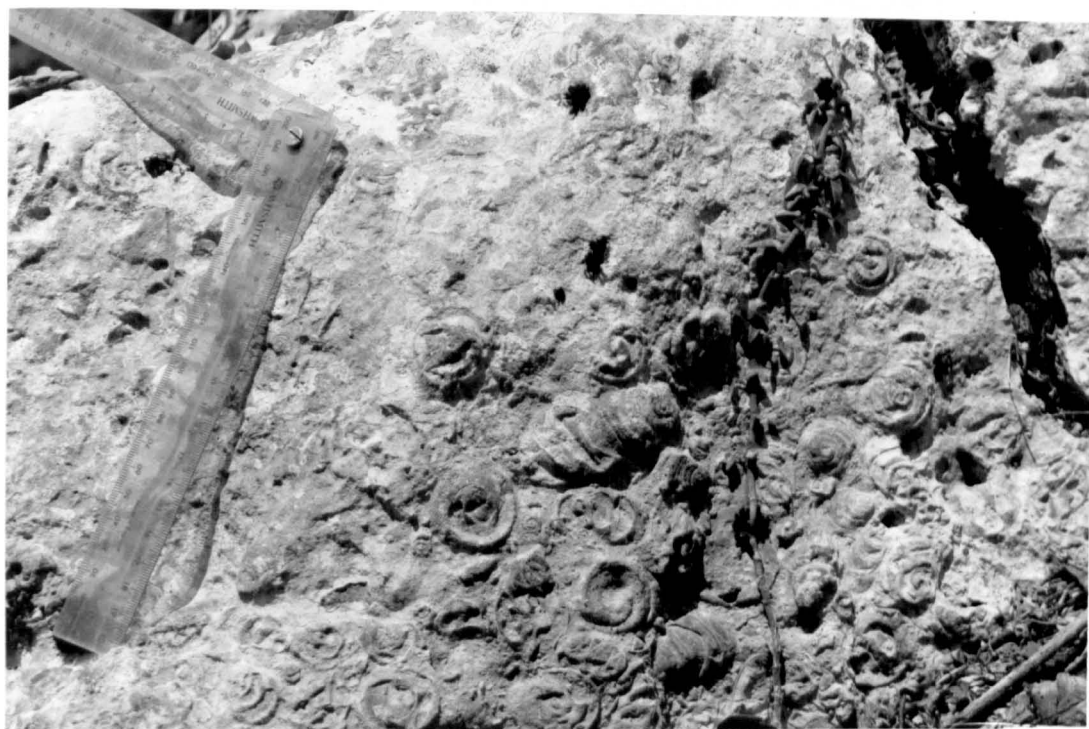


Figure 4.5 Dense concentrations of *Phaneroptyxis africurgonia* in Lower Aptian strata at Lagarde d'Apt, France.

*Nerinella* species 1, an extremely acicular form occurs in orbitoline marls, together with brachiopods, echinoids, bun corals, various bivalves and other gastropods, mainly naticids and cerithiids (locality 61, Ericeira Port, Portugal). These beds form part of the Marno-calcaires à *Heteraster oblongus* (Lower Bedoulian, Lower Aptian) and are considered to represent a restricted lagoonal environment where energy was low and sedimentation was affected by terrigenous influx (Rey, 1979), although the presence of stenohaline groups such as corals, brachiopods and echinoids indicates normal salinity. A similar situation occurs in the Albian at Praia do Sol (locality 69) Ericeira, Portugal, where *Multipityxis dolomieui* (Choffat) occurs in marly sediments as part of a very diverse molluscan assemblage including oysters and cerithiids, which is again thought to represent deposition within a lagoonal environment (Rey, 1979). At La Gabelle, France (locality 20 - Bedoulian, Lower Aptian) G1 species 1 forms a dominant element in a mixed fauna containing rhynchonellid brachiopods, serpulids,

bivalves (*Exogyra*, *Pterotrignia*, *Neithea*), small gastropods (probably Procerithiidae) and echinoids within a medium grained silty sediment thought to represent offshore prelittoral deposits (Masse, 1976).

Nerinellidae genera appear, therefore, to have been more tolerant of lower energy environments occurring in both lagoonal and prelittoral situations, where marly and silty sediments predominated. Nerinellids do occur in carbonate sediments, but they are relatively rare, forming only a small part of the overall nerineid fauna. Wieczorek (1979) records nerinellids within all carbonate sediments in which nerineids occur, indeed the group apparently forms one of the dominant genera in oolitic limestones. The differences between Upper Jurassic and Lower Cretaceous Nerinellidae ecology may reflect the development of habitat partitioning between major nerineid groups during the Cretaceous.

Nerinellids often show strong current orientation (eg localities 20 and 68, figure 4.6) even when shell preservation is good and a wide size range present. Their shell morphology seems to have made this group very sensitive to currents during life, and this may indicate an infaunal habit (see section 4.2.7). The dense mono-specific lenses of *Nerinella algarbiensis* (Choffat) (figure 4.7) which occur at Praia da Luz, Portugal (locality 68, Aptian/Lower Albian) imply an opportunistic development in this situation.

Although most abundant in carbonate facies, *Eunerinea* species are not restricted to these, but also occur in foram or oyster marls (localities 41, 51 and 52) related to low energy restricted environments (Salas, 1984; Rey, 1979). Preservation is usually very poor in these sediments (locality 52 is an exception) making specific determination impossible; it is also difficult to assess the likelihood of transport, although the large size of specimens would tend to discount this possibility. *Prygmatis* species (locality 52) and, very rarely, *Pchelinsevia* species (locality 41) also occur in these sediments. Allison (1955) reports the presence of nerineids in oyster biostromes of Aptian/Albian sediments of Baja California and Carbone and Sirna





Figure 4.6 Orientation of *Nerinella algarbiensis* in Aptian strata at Praia da Luz - such orientation is common in nerinellid species, indicating that their acicular shape rendered them very sensitive to currents.



Figure 4.7 Densely packed mono-specific lenses of *N. algarbiensis* (same locality as in figure 4.6)

(1981) mention the occasional occurrence of nerineids in oyster and foram wackestones in Cenomanian and Turonian deposits in Central Italy.

#### 4.9.2 Small Gastropod Assemblages

At two localities (35, Combovin, France, and 47, Arribida, Portugal) nerineids, usually small in size, have been found associated with extremely dense concentrations of *Trochacteon*, and various other gastropods (see Sayn, 1932). The nerineid genera present in both cases are *Ptygmatis*, *Aphanoptyxis* and *Nerinella*. The associated sediment is a medium/fine grained silt, but more or less complete molluscan shells form the bulk of the bed (figure 4.8). At locality 47, the sediments above and below are of terrestrial origin, so it appears that the fossiliferous band represents a brief marine incursion (D. C. Kitson, pers comm) a very nearshore situation is therefore indicated. The association has also been interpreted as marginolittoral in France (Masse, 1976, p 423). The shells show excellent preservation and there is wide size



Figure 4.8 Dense concentrations of small nerineid and other gastropod shells. Mid/Upper Barremian, Arriba Pool, Portugal.



variation present; these deposits probably represent an abundant fauna which has been preserved in situ under the concentrating action of winnowing currents and slow sedimentation rates. The variety and type of fauna does not indicate that abnormal salinities were operating. There are some similarities between these associations and the fauna of the Punfield Marine Band, although the only nerineids recorded from the latter are two questionable *Nerinea* species and a *Pseudonerinea* (Cleevely, Morris and Bate, 1983).

#### 4.10 PALAEOSALINITY

In the vast majority of cases there is clear evidence that the Nerineacea inhabited normal marine environments whether the conditions were open marine or rather more restricted; co-occurrence of varied fauna, including typically stenohaline groups such as corals and brachiopods, confirm the existence of normal salinities.

There is evidence from Lower Aptian strata (Bedoulian/Gargasian) in Portugal that small *Ptygmatis* specimens occur as the only macrofossil within sediments which are transitional to terrestrial deposits (D. C. Kitson, pers comm). The juxtaposition of these sediments, and the severely restricted nature of the macrofauna may reflect abnormal salinities which apparently *Ptygmatis* could tolerate. The specimens are small, which may also result from variable salinity (Vermeij, 1973); such a size relationship has been observed in *Cerithium* species inhabiting intertidal, rather than subtidal environments (Houbrik, 1974). A single small *Ptygmatis* specimen is reported from bauxitic deposits of Barremian/Aptian age, associated with *Pyrazus* and *Cimolithium*, in an apparently brackish lagoonal environment (Combes and Mongin, 1970). In other occurrences of apparently autochthonous nerineids occurring in situations where abnormal salinity is indicated (P. M. Ellis, pers comm; M. P. Watkinson, pers comm) *Ptygmatis* is again the genus involved.

It has been suggested (Herm, 1977; Herm, Kauffman and Wiedmann, 1979; Fürsich and Schmidt-Kittler, 1980; Kollmann and Summesberger, 1982) that nerineids were generally tolerant of abnormal salinities, for example:- "..... euryhaline mollusks disappear and are replaced by typical brackish water groups such as *Polymesoda*, *Nerinea* and *Glaucania*" (Herm et al, 1979, p 38). This suggestion is based on Upper Jurassic facies from Portugal (Fürsich and Schmidt-Kittler, 1980) and Upper Cretaceous Gosau deposits of Austria (Herm, 1977; Herm et al, 1979; Kollmann and Summesberger, 1982). Fürsich and Schmidt-Kittler base their proposal on the occurrence of nerineid shell beds containing *Valanginella* and *Trochaliopsis* in fine/medium grained marly sediment in association with *Eomiodon*, a bivalve which appears to have been extremely tolerant of abnormal salinities, however, it is noted that many of the nerineids show signs of wear:- "frequent reworking and/or large scale transport seems to have taken place" (p 970). There does not appear to be evidence of autochthonous nerineid shell beds developing alongside mono-specific *Eomiodon* horizons which would provide unequivocal evidence of nerineids inhabiting water of abnormal salinity. *Eomiodon* also forms part of mixed assemblages thought to indicate normal salinities, and it is likely that the nerineids lived in such environments only forming concentrated shell bands in areas of abnormal salinity as a result of postmortal transport.

The association of nerineids with "brackish water facies" has been persistently cited in literature covering the Gosau deposits of the Upper Cretaceous of Austria. This association has been based on the inferred salinity tolerances of the associated fauna (eg Kollmann, 1967 on *Trochacteon*; Schenk, 1972 on various gastropods). Forms cited as indicating reduced salinity (eg *Neritopsis*, *Pseudomelania*, *Cassiope*, Herm, 1977; Kollmann and Summesberger, 1982) are not exclusively or even predominantly brackish water inhabitants (N. J. Morris, pers comm) and the results of carbon and oxygen isotope studies of aragonitic shell material from various Gosau deposits all indicate that the nerineids were living in normal marine conditions (see below).

Despite frequent repetition in the literature, the assumption that nerineids of the Gosau deposits were living in brackish water appears to have little evidence to support it.

The Nerineacea were largely confined to seawater of normal salinities, although certain genera, namely *Ptygmatis*, seem to have been able to tolerate abnormal or fluctuating salinities which allowed them to form a part of the low diversity faunas that developed in such situations.

#### 4.10.1 Isotope Measurements

The use of carbon and oxygen isotope values to infer palaeosalinities and palaeotemperatures is well established (Arthur et al, 1985). The principle depends on the differential composition, with respect to C and O isotopes, of freshwater and seawater. Freshwater is relatively poorer in  $^{13}\text{C}$  and  $^{18}\text{O}$  than seawater. If shell material is precipitated in equilibrium with the surrounding water, and the isotopic composition of the shell remains unchanged, then the value of  $^{18}\text{O}/^{16}\text{O}$  and  $^{13}\text{C}/^{12}\text{C}$  can be used to estimate water salinity at the time of shell deposition (Allen et al, 1973). However, as the precipitated  $^{18}\text{O}/^{16}\text{O}$  ratio is also considerably affected by temperature as well as palaeosalinity, the oxygen isotope value is generally used to infer palaeotemperatures and carbon isotope values to evaluate water composition.

If isotopic values are to be used in palaeoenvironmental studies, it has to be assumed that :-

- 1 shell material was actually precipitated in equilibrium with original water composition
- 2 the original isotopic composition has been preserved

With respect to 1, although it has been found that certain organisms such as corals and echinoids exert a considerable vital effect on skeletal isotope composition, it appears that molluscs, in general, precipitate C and O in isotopic equilibrium with the surrounding water (Arthur et al, 1985). Also the generally good correlation between

isotopic values from different organisms collected from the same locality (see table 4.2) indicates that vital effects are not significant (Tan and Hudson, 1974).

To ensure that the original isotopic composition has been preserved, it is essential that original shell material is present. The specimens used in this study all showed aragonitic preservation, tested using standard procedures with Feigl's solution (Friedman, 1959; Warne, 1962). Tan and Hudson (1974) also note that consistent results between co-occurring fossils and "reasonable" palaeotemperatures calculated from  $^{18}\text{O}/^{16}\text{O}$  values indicate that original isotopic composition is present. Both of these criteria are met by the majority of the results of this study. In any case, the effect of diagenetic alteration is to reduce both  $^{13}\text{C}/^{12}\text{C}$  (Allen et al, 1973) and  $^{18}\text{O}/^{16}\text{O}$  (Stanton and Dodd, 1970), which would, respectively, give spurious results of greater freshwater influence and higher temperatures. Results which show marine salinities therefore provide strong evidence of original water composition.

The strict criteria of original aragonitic shell preservation has restricted the selection of specimens for analysis, for example, no aragonitic material was available from the Schneckwand, near Russbach, Austria, a very famous locality which is cited as containing brackish water fauna (Kollman and Summesberger, 1982). Further details of the localities where material has been collected from are given in Appendix 1 and most are discussed by Kollmann and Summesberger (1982).

In addition to material from the Gosau deposits proper, four specimens from well-established non-marine environments (N. J. Morris pers comm) of the Upper Cretaceous of Hungary and France were also analysed for comparison.

The carbon and oxygen isotopic values were determined by Dr Monica Grady of the Open University, using standard analytical procedures (see Lloyd, 1969; Tan and Hudson, 1974; Grady, 1987). The interpretation of results also followed standard practices. Palaeotemperature was calculated using:-

$$t (^{\circ}\text{C}) = 19 - 3.52(\Delta_{\text{C}} - \Delta_{\text{W}}) + 0.03 (\Delta_{\text{C}} - \Delta_{\text{W}})^2$$

where  $\Delta_c = \Delta^{18}\text{O}$  of  $\text{CO}_2$  generated from carbonate at 25°C (PBD)

$\Delta_w = \Delta^{18}\text{O}$  of  $\text{CO}_2$  generated in equilibrium with water at 25°C (SMOW)  
(taken to be -1.2‰ after Grady, 1987)

this formula was developed by Grossman and Ku, 1981 (reported in Arthur et al, 1985) for use with aragonite-water systems.

#### 4.10.2 Discussion

The palaeotemperatures calculated from  $\Delta^{18}\text{O}$  are all within ranges present in shallow tropical waters of the present day; Houbriek (1974) for example, has recorded an average temperature of 25.3°C with a maximum of 33°C in Tampa Bay, Florida. Lowenstam and Epstein (1954) note that temperatures up to 35°C have been recorded in shelf seas with restricted circulation. The majority of palaeotemperatures are reasonably consistent with the overall palaeoenvironment and therefore provide further evidence that original isotopic compositions have been preserved.

The criteria:-

$$\Delta^{13}\text{C}/\text{‰} > -2\text{‰} = \text{marine}$$

with brackish water overlap

$$\Delta^{13}\text{C}/\text{‰} < -2\text{‰} = \text{freshwater}$$

are generally used for the interpretation of palaeosalinities based on carbon isotope data (Allen, Keith, Tan and Deines, 1973; Keith, Anderson, Eichler 1964; Tan and Hudson, 1974). If these criteria are applied to the Gosau results, most specimens (including all the nerineids and trochacteons) have C isotope ratios that are wholly consistent with normal marine salinities. The exceptions are two *Cassiope* specimens (nos 3 and 17) which have values approaching the limit of -2‰, indicating that they probably inhabited brackish water, and a *Pyrgulifera* species which has a very low

Specimen	No	Locality	Age	$\Delta^{13}\text{C}$	$\Delta^{18}\text{O}$	Palaeotemp	Palaeosalinity
<i>Simploptyxis</i> <i>?buchi</i>	1	Lanzing	?U. Santonian/ L. Campanian	+6.04	-3.49	27.1	marine
<i>Trochateon</i>	2	"	"	+9.28	-3.00	25.4	marine
<i>Cassiope</i> <i>lanzingensis</i>	3	"	"	-1.21	-3.66	27.7	marine/brackish
<i>Turritella</i>	4	Gosau (Edlbach) <sup>1</sup>	Santonian	+0.51	-3.75	28.1	marine
naticid	5	"	"	+1.15	-2.86	24.9	marine
bivalve	6	"	"	+1.14	-2.80	24.7	marine
<i>Neritella</i>	7	Russbach	Santonian	+1.54	-6.19	36.7	marine
<i>Trapezium</i>	8	"	"	+1.05	-3.78	28.2	marine
naticid	9	"	"	+0.32	-2.36	23.1	marine
<i>Turritella</i>	10	"	"	+1.29	-3.87	28.5	marine
mytiloid	11	"	"	+4.15	-2.14	22.3	marine
<i>Trochacteon</i> <i>?larmarki</i>	12	Gams die Noth	U. Coniacian/ Santonian	+2.61	-4.77	31.7	marine

<sup>1</sup>*Neritella* co-occurred but there were no specimens with aragonite preservation available for analysis

Table 4.2 Carbon and oxygen isotope data of various species collected from Upper Cretaceous Gosau deposits or similar strata. Inferred palaeotemperatures and palaeosalinities are based on the data.

Specimen	No	Locality	Age	$\Delta^{13}\text{C}$	$\Delta^{18}\text{O}$	Palaeotemp	Palaeosalinity
<i>Simploptyx</i> <i>?buchi</i>	13	Zottbach	Coniacian/ Santonian	+4.94	-3.78	28.2	marine
<i>Trochacteon</i> <i>?lamarki</i>	14	"	"	+5.19	-3.82	28.3	marine
naticid	15	"	"	+0.90	-3.10	25.7	marine
<i>Terebraliopsis</i> <i>articulatum</i>	16	"	"	+0.59	-3.48	27.1	marine
<i>Cassiope</i> <i>bicostata</i>	17	"	"	-0.69	-7.12	40.0	marine/brackish
<i>Pyrgulifera</i>	18	"	"	-4.01	-5.70	34.9	freshwater
<b><u>KNOWN NON-MARINE FAUNA</u></b>							
<i>Pyrgulifera</i> <i>pichleri</i> BM(NH)G10438	19	Ajka, Hungary	U. Cretaceous	-3.50	-4.30	30.0	freshwater
<i>Bulimus</i> <i>munieri</i> BM(NH) G10429	20	Ajka (Bakony) Hungary	U. Cretaceous	-3.28	-3.10	25.7	freshwater
<i>Dejanira</i> <i>biranrinata</i> BM(NH) G10436	21	Bakony Hungary	U. Cretaceous	-1.81	-3.69	27.8	freshwater/brackish
"Trocho- morpha"	22	Langesse S. France	U. Cretaceous/ L. Danian	-12.88	-4.99	32.5	freshwater

Table 4.2 Carbon and oxygen isotope data of various species collected from Upper Cretaceous Gosau deposits or similar strata. Inferred palaeotemperatures and palaeosalinities are based on the data.

$\Delta^{13}\text{C}$  value, clearly indicating a non-marine habitat. The known non-marine specimens (nos 19 - 22) show considerably lower  $\Delta^{13}\text{C}$  values than those of the Gosau specimens (apart from the exceptions noted above), whereas their  $\Delta^{18}\text{O}$  values are not distinct. This emphasises the relevance of using  $\Delta^{13}\text{C}$  in palaeosalinity assessments.

The only abnormal palaeotemperatures are shown by nos 7, 17, 18 and 22. The temperature in all cases is higher than expected and may therefore reflect diagenetic alteration and/or non-marine salinities. Where normal marine salinities are indicated by  $\Delta^{13}\text{C}$  (eg no 7 - *Nerinella* species) a diagenetic explanation is most probable; diagenesis would also have caused a lowering of  $\Delta^{13}\text{C}$  value, although the value for no 7 is still within the marine salinity field. In nos 17, 18 and 22, a brackish or freshwater habitat is indicated by the  $\Delta^{13}\text{C}$  values and this would have a corresponding effect of lowering  $\Delta^{18}\text{O}$ , and therefore causing a higher apparent palaeotemperature.

The average temperature given by these results, excluding the abnormal figures discussed above, is 26.9°C. This is slightly higher than the average temperature of 25.3°C reported from present day shallow tropical waters (Houbbrick, 1974).

#### 4.10.3 Conclusions

Isotopic data shows that the Gosau nerineids and trochacteons lived in water of normal marine salinity. *Cassiope* and *Pyrgulifera* show evidence of brackish or freshwater associations, but the results obtained for other Gosau molluscs all indicate a marine habit.



#### 4.11 PALAEOGEOGRAPHY

The restricted distribution of nerineids, together with their frequent association with corals and rudists indicates that the superfamily inhabited exclusively warm water environments. The Nerineacea were largely restricted to the Tethyan Realm, representing the Mesozoic "tropics" and formed a very characteristic part of the Tethyan fauna. Transitional faunas from the edge of Tethys do not contain nerineids (Sohl, 1971), although they did occur as far north as Britain during periodic climatic warming events. Kollmann (1978) reports rare *Aphanoptyxis* species from marginal locations in the Paris Basin during the Lower to Mid Cenomanian; this implies that *Aphanoptyxis* was slightly more tolerant of cooler conditions, although the occurrence probably also reflects a localised warming event which was evidently not pronounced enough to allow the spread of other nerineid genera.

Although palaeogeographic trends within the group have not been studied in detail, a worldwide distribution (within tropical and subtropical seas) is indicated. Yin (1962) and Wen (1983) report typical nerineid genera respectively from Upper Jurassic and Cretaceous strata of Tibet; Cretaceous nerineids are also described from Japan (Hayami and Kase, 1977). The nerineid faunas of North and South America are mentioned periodically in the literature, although thorough description and evaluation of the material available is sadly lacking. Where known, the American fauna appears to be close to that of Europe and the Middle East (Sohl, 1971). The European/North African/Middle Eastern/Eastern Russian nerineid fauna is the most extensively studied and well-documented in the world; similar faunas, at least in the Lower Cretaceous are reported from Pakistan (Rossi Ronchetti, 1956; Ichikawa and Maeda, 1965). The worldwide distribution of the group supports the concept of the Tethyan faunal realm extending around the globe (Kauffman, 1973).

The Nerineacea occur in a wide circum-global belt which closely conforms to the inferred limits of the Tethyan realm (see Sohl, 1987, figure 1); occurrences of

nerineids in higher latitudes are thought to reflect warming events which periodically allowed the expansion poleward of tropical and subtropical climatic belts.

#### **4.12 OVERALL CONCLUSIONS**

Most nerineids were probably mobile epifaunal herbivorous gastropods inhabiting a variety of mainly carbonate-dominated environments. They lived in well-oxygenated, warm, clear, shallow water of normal marine salinity, within a range of energy levels. Their distribution was restricted to tropical and subtropical areas; they appear to have been intolerant of cool conditions.

During the Lower Cretaceous, there appears to have been wider exploitation of shallow marine habitats than in the Upper Jurassic, with the development of habitat partitioning between genera with *Nerinella* and *Ptygmatis* particularly exploiting more restricted environments that were evidently unavailable to other genera. In the Upper Cretaceous, as rudists become predominant as the main frame-building organisms, nerineids show a decreasing association with biogenic build-ups, becoming more associated with either inshore sandy environments or deeper offshore facies.

## CHAPTER 5

### EVOLUTION AND PHYLOGENY

#### 5.1 INTRODUCTION

Historically, the amount of attention that the Nerineacea have received has been extremely low compared to other groups of similar diversity levels and distribution patterns such as the rudists. The documented fossil record is therefore correspondingly limited and nerineacean taxonomy is in a relatively primitive state.

However, even within the present level of knowledge, it is possible to assess some aspects of the overall evolution of the group; its origins, diversification and extinction patterns, and to speculate upon the possible causes of these.

The connections between systematic division and phylogeny are not well-established. A complex of superficially conflicting character arrays has hindered the perception of evolutionary trends and relationships. In this chapter, the distinguishing criteria used at various taxonomic levels are reviewed, and the possible evolutionary pathways discussed and evaluated.

#### 5.2 ORIGINS, DIVERSIFICATION AND EXTINCTION

The earliest reported occurrences of nerineacean species are from the Liassic (Lower Jurassic). The genera reported (Dietrich, 1925) are *Nerinella*, "*Nerinea* ss" (= *Eunerinea*), ?*Aptyxiella*, *Pseudonerinea* and *Böhmiola*, although the latter genus is regarded as questionable (Wenz, 1940). *Nerinella* is the most diverse genus, with six species recorded in the Lias, as opposed to one or two species belonging to each of the

other genera. The Nerineacea seem therefore to have arisen during the very latest Triassic or very early Jurassic, and developed modest diversity levels during the Liassic. More work is needed to elucidate the stem group; the reports of early occurrences tend to be poorly defined both stratigraphically and taxonomically, and there is no clear evidence of which features are primitive. At present, *Nerinella*, with its relatively high early diversity and early appearance in the Hettangian (*Nerinella grossouvrei* Cossmann; Cossmann 1896 and 1898) seems to be the most likely candidate for the ancestral form.

During the Middle Jurassic, nerineacean diversity (at generic level) generally increased, although an extinction event occurred in the Callovian, after which diversity continued to rise almost explosively during the late Jurassic to reach a peak at the end of the period (Tithonian) (Barker, 1976). Generic diversity declined markedly in the early part of the Lower Cretaceous, and then continued to show a more gradual decline throughout the rest of the Cretaceous (Barker, 1976).

Specific diversity of the Cretaceous (reported by Sohl, 1987) shows a somewhat different pattern (figure 5.1), with high diversity persisting from the beginning of the Cretaceous to Mid-Valanginian times, then a progressive and marked reduction until the Mid-Barremian. This is followed by a rise in diversity through the latter part of the Barremian and Aptian which continues, at a reduced rate until the Mid-Cenomanian when a Cretaceous species diversity peak occurs. There is a severe decline in species numbers from the Mid-Cenomanian to the Turonian/Coniacian boundary, leaving only a remnant fauna, which is further reduced during the Coniacian, Santonian and Early Campanian; only a few species survive through the Campanian and Maastrichtian. The group appears to have become completely extinct by the end of the Maastrichtian.

### 5.2.1 Causes of Extinctions

As inhabitants of exclusively warm water, shallow environments, nerineids would have been extremely sensitive to any large scale changes in temperature or sea level. The restricted distribution of nerineids (Section 4.9) indicates that the group was intolerant of cooler temperatures. Changes which affected the abundance of shallow marine habitats, particularly those where deposition was primarily carbonate, would also have profoundly affected nerineids.

Barker (1976) has attributed the decline in generic diversity during Callovian times to the widespread replacement of carbonate sediments by clayey facies throughout Europe in the course of this stage.

Specific diversity levels show two episodes of decline during the Cretaceous (Sohl, 1987; figure 5.1). There is a rather slow decline in species numbers from 40 to 20 which starts during the mid-Valanginian and continues until the mid-Barremian. The gradual nature of this trend, extending over about 12 million years does not indicate an abrupt extinction event. The lowering of specific diversity may reflect a general decrease in carbonate facies, at least in certain areas of southern Europe during the Hauterivian. This is related to a marine transgression which restricted the development of coral-rudist buildups (Masse and Philip, 1981) with which most nerineid genera were associated in the Lower Cretaceous (Section 4.10) and Skelton (1985) has recorded a drop in rudist diversity during the Hauterivian

However, the decline in nerineid species during this period may also reflect the effect of "monographic bursts" covering the fauna of the Valanginian and Barremian (especially the Upper Barremian) strata, but not the Hauterivian. The nerineid species of Valanginian age have been studied and described by Choffat (1896 - 98) and Pchelintsev (1965) and Barremian/Aptian nerineids (especially those of the urgonian facies of the Upper Barremian) have been described by Coquand (1865), Cossmann (1907 and 1916), Sayn (1932) and Delpey (1939); all of these sources have been used

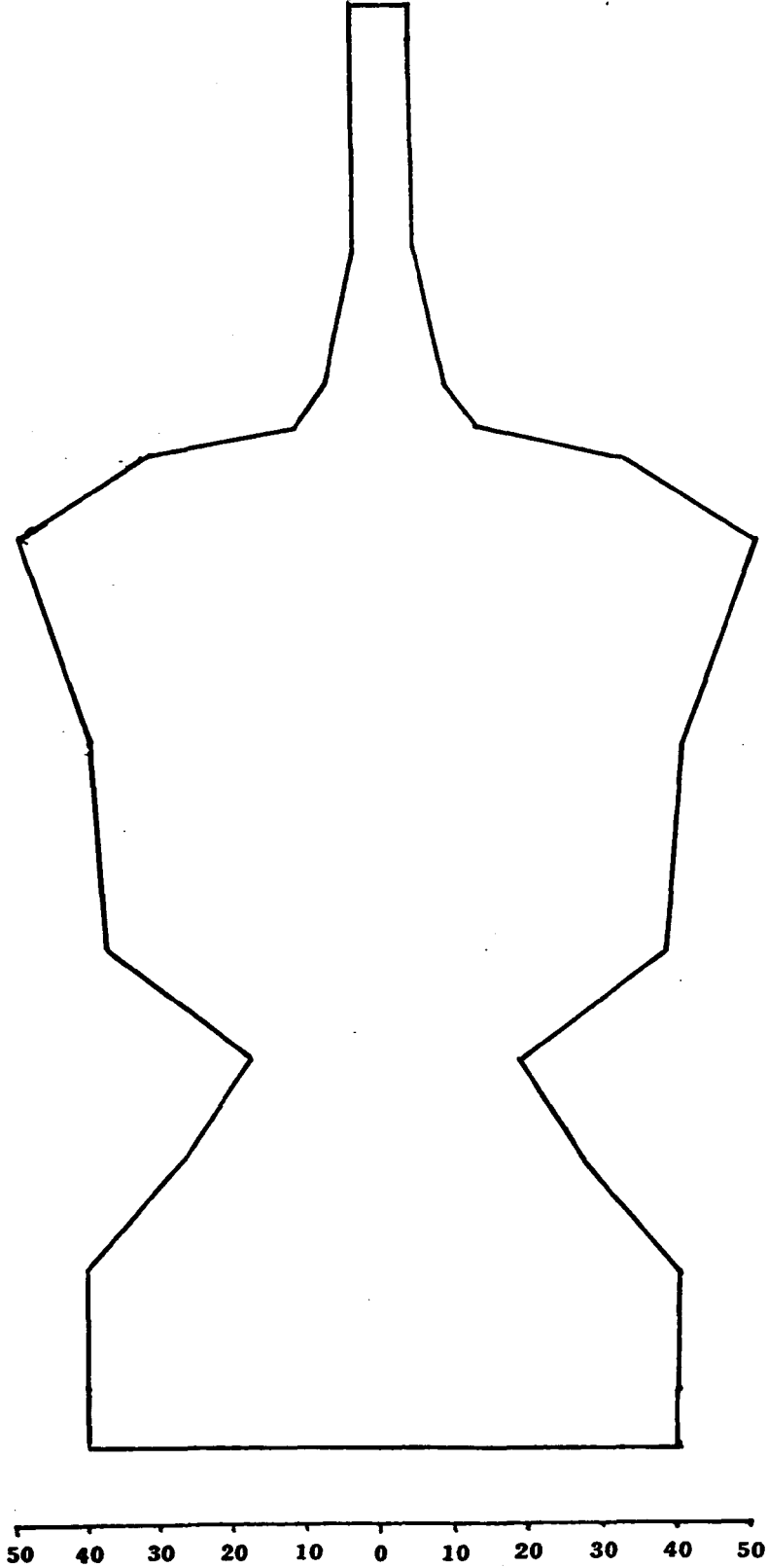
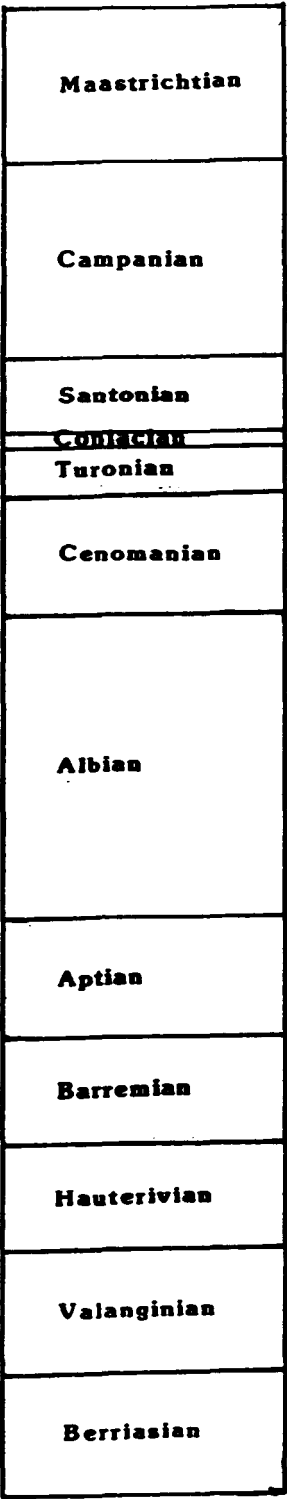


Figure 5.1 Nerineacean species diversity during the Cretaceous (excluding the Ileriidae) after Sohl, 1987.

by Sohl, 1987. Hauterivian nerineids are relatively scarce in the literature, although the present study has found a moderately diverse nerineid fauna in Hauterivian strata (localities 45 and 59) in Portugal, which includes a number of species previously reported only from Barremian sediments. This marked but gradual decline in nerineid diversity during the Neocomian therefore may have been produced by both a reduction in available habitat (particularly as this occurred in areas where nerineid taxonomic study was subsequently heavily concentrated) and poor coverage in the literature of Hauterivian nerineaceans.

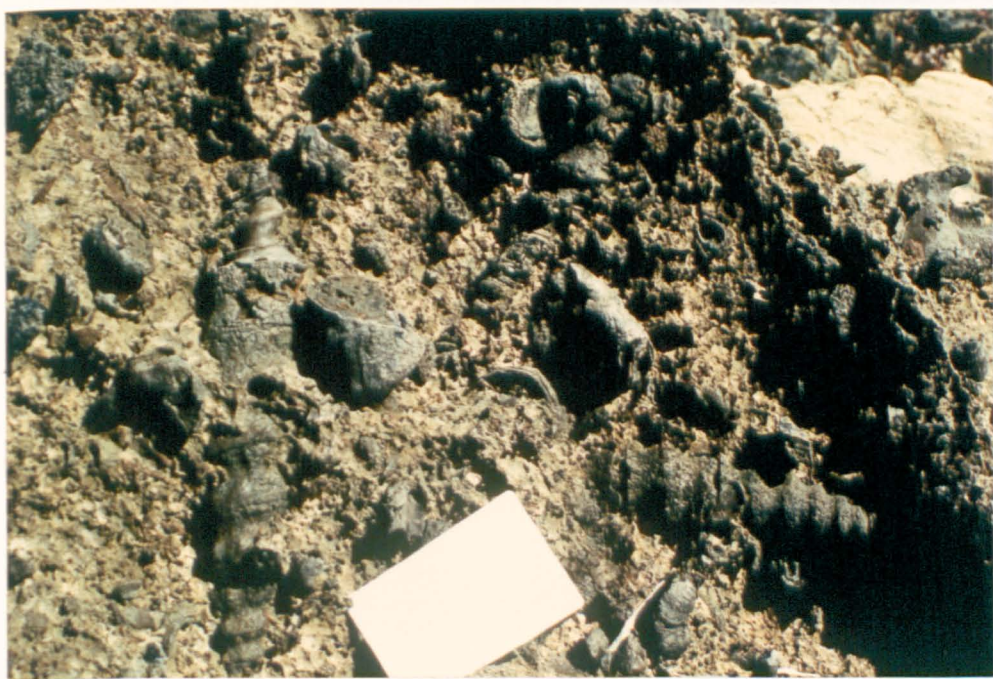


Figure 5.2 Hauterivian nerineids - part of an abundant and diverse nerineacean fauna occurring at locality 45 (Silicified Locality) S of Crismina, Portugal

There is an abrupt drop in species numbers from 50 to about 10 from the mid-Cenomanian to the Turonian/Coniacian boundary, a period of around 5.5 my. This decline is much more marked, and occurs more quickly than the Lower Cretaceous decline. It almost certainly reflects a true rise in extinction rates for nerineids, and may have resulted from large scale environmental changes that occurred in the marine biosphere during this period. Kauffman (1984) has reported two major extinction

events during this time; at the Cenomanian/Turonian boundary (commencing in Late Cenomanian times, 93 - 91 my) and the Turonian/Coniacian boundary (89.3 - 89 my). Both are considered to result from abrupt eustatic sea level rises accompanied by increased temperatures and oxygen depletion events in deeper waters (Kauffman, 1984). Perhaps the most significant effect of these widescale environmental changes for the Nerineacea may have been the abrupt environmental changes in shallow marine environments that accompanied a sudden marine transgression.

The period covering the Late Cenomanian to the Upper Turonian/Coniacian boundary represents the most significant extinction episode for nerineaceans during the Cretaceous. The final extinction of the group in the late Upper Cretaceous involved only a remnant of surviving species. The Nerineacea are often cited as one of the many major "victims" of the Cretaceous-Tertiary extinction event. Although the group probably did become totally extinct during the Maastrichtian, only very few representatives actually survived to this stage as diversity had already been severely reduced by earlier events. Suggestions that the nerineids became extinct at "a Maastrichtian peak in their radiation" (Kauffman, 1984, p 172) are therefore extremely misleading.

### 5.2.2 Post-Coniacian Nerineids

There are relatively few reports of nerineids from strata younger than Coniacian worldwide, although in particular areas (for example the Gosau deposits of Austria), Upper Cretaceous forms have been extensively studied. Three genera are reported from Gosau (Coniacian/Santonian) sediments:- *Plesioptygmatis* (*Simploptyxis*), *Vernedia* (= *Itruvia* after Kollmann and Sohl, 1979), and *Nerinella*<sup>1</sup> (Teidt, 1958;

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<sup>1</sup>The generic names used by various authors show some variation; the terms used here are considered to be the most "correct", in relation to both nomenclatural rules and taxonomic interpretation.





Figures 5.3a and b *Plesioptygmatis pailleteana* d'Orbigny from the Gosau deposits of Austria. An example of one of the three genera to survive beyond the Coniacian..

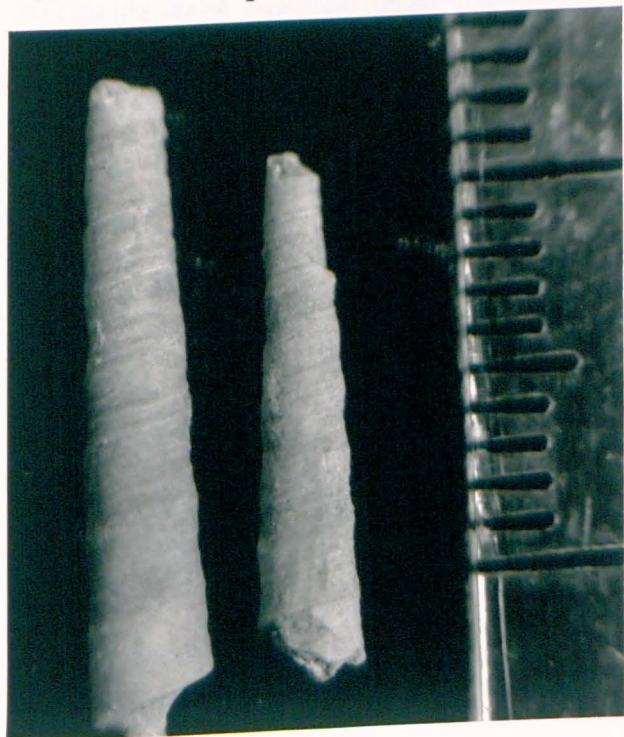


Figure 5.3c *Nerinella ?flexuosa* Sowerby. A second genus that survived into the Maastrichtian.

Kollmann, 1967a; Rahman, 1967); the same genera (excluding *Nerinella*) are reported from Turonian strata of the USSR (Pchelintsev, 1954).

*Plesioptygmatis* species are reported from Senonian strata (Cardenas beds) of Cuba (Böse, 1906; Knipscheer, 1938) which are reported to be Maastrichtian (Knipscheer, 1938) and Sohl (1987) figures an undescribed *Nerinella* species from the Maastrichtian of Puerto Rico. Stoliczka (1868) recorded a *Vernedia* (= *Itruvia*) species from the Arrialoor group of Trichinopoly, southern India; this group is Campanian and Maastrichtian in age (Kollmann and Sohl, 1979). This rather sparse evidence implies that only three genera survived the Turonian/Coniacian, and that only two of these definitely survived into the Maastrichtian - *Nerinella* and *Plesioptygmatis*. The only unequivocal reports of Maastrichtian nerineids come from the Caribbean region, which may have become a "refuge" area where nerineids persisted into the latest Cretaceous, after becoming extinct elsewhere. According to Sohl (1987, p 1101) "some species remain incredibly abundant locally and remain formers of lenticular rock masses into Maastrichtian times in areas like Puerto Rico"; such abundances have not been reported in Maastrichtian strata elsewhere in the world.

Nerineids have been reported from the Maastrichtian type locality in Holland (Binckhorst, 1973; Kaunhowen, 1898) but these reports are not well substantiated by the material available, for example, Kaunhowen describes a "*Nerinea*" species based on a broken section of columella which has folds and Binckhorst bases a "*Nerinea*" species on an internal mould.

Several reports of "*Nerinea*" from the Upper Cretaceous involve Campanilidae species:-

eg "*Nerinea ganessa*" Noetling

Noetling, 1897 - Pakistan  
Douville, 1916 - Maastrichtian, Tibet  
Greco, 1916 - Maastrichtian, Egypt  
Lees, 1928 - Maastrichtian, Oman  
Guitani, 1947 - ?Maastrichtian, Libya

*"Nerinea fournieri"* Vidal

Vidal, 1917 - Maastrichtian, Spain  
Bataller, 1949 - Maastrichtian, Spain

or some other clearly non-nerineid gastropod:-

*"Nerinea quettensis"* Noetling (1897) - ?Maastrichtian, Pakistan

or other questionable identification made on poorly preserved material:-

*"Nerinea supracretacea"* Bellardi (1852), ?Eocene, France.

The shell shape of the Campanilidae and the common occurrence of internal folds in this family have caused this confusion with the Nerineacea. However, there is no systematic relationship between the two groups (Chapter 6; Houbrick, 1981).

Some Middle Eastern (Oman) Maastrichtian deposits which might reasonably be expected to contain nerineids (ie Tethyan, shallow water sediments) do not, but do contain abundant large campanilids (P. W. Skelton, pers comm). Campanilids appear to have been largely tropical, shallow water, epifaunal algal grazers (Houbrick, 1981) and may have succeeded the nerineids in this ecological niche. According to Delpey (1941), campanilids first appear in the Cenomanian and achieved considerable diversity by Maastrichtian times.

### 5.3 EVOLUTIONARY TRENDS AND TAXONOMY

#### 5.3.1 Major Groupings

Nerineid genera were split into three major families by Cossmann (1896). This followed the erection of the Nerineidae by Zittel in 1873. Cossmann's action brought together the Ceritellidae (=Tubiferidae), containing genera which had not been closely associated previously with the nerineids, and the Nerineidae; the family Itieriidae was set up to receive ovate nerineid genera with overlapping whorls that had previously been included in the Nerineidae by Zittel. This tripartite division of the Nerineacea is now well-established. Pchelintsev (1968) proposed a further separation of a nerinellid group from the above families. Extremely acicular genera are quite widely separated morphologically from other more conically shaped forms, and the former do seem to represent a distinctive grouping. The author supports the separation of acicular forms to give a fourth major grouping within the Nerineacea, but considers that Pchelintsev's inclusion of certain conically shaped genera within this grouping to be unsatisfactory (see Chapter 2 for further discussion).

It seems probable that three of the four groups were present during the Early Jurassic, with perhaps the acicular nerinellids being the very earliest nerineids. The last group, the itieriids, seem to have been derived from the Nerineidae; *Phaneroptyxis* (first occurring in Bathonian strata, Pchelintsev, 1968) appears to be an intermediate form (Rahman, 1967), where the envelopment of previous whorls occurs, but to a much lesser degree than occurs in *Itieria* (appearing in the Oxfordian, Rahman, 1967). The four major divisions of the Nerineacea appear to be distinct and to reflect true phylogenetic separation.

The perception of systematic relationships at levels below those of the major groupings has been extremely limited. Workers have been hampered by the incompleteness of the

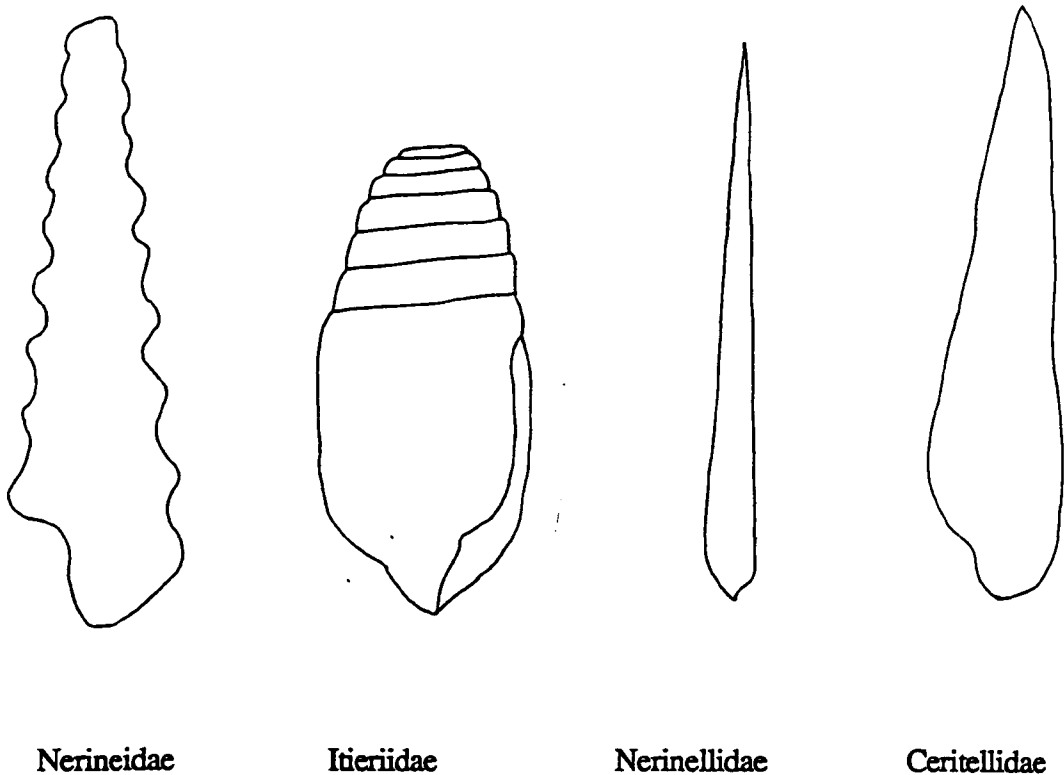


Figure 5.4 Gross morphologies of the four Nerineacea families.

recorded material available, a problem made more acute by the lack of study accorded to nerineids compared to other similar fossil groups. The inconsistency and unreliability of the taxonomy which has developed also makes the perception of evolutionary relationships difficult. Some workers have expressed their frustrations quite openly :-

"Ich habe die Ergebnisse meiner mühevollen und ziemlich undankbaren Untersuchungen....."

(I have organised the results of my laborious and rather thankless research ..... )  
Zittel, 1873, p 219.

Others have developed and used methods which give a purely functional classification with no pretence of reflecting systematic relationships (Dietrich, 1925; Delpey, 1939; Cox, ms circa 1953). Pchelintsev's (1968) complete revision of the whole group

presents some profound inconsistencies in the application of criteria used for systematic association and distinction (own observations; Barker, 1976).

The difficulties associated with nerineid taxonomy have derived mainly from confusion as to which characters are most significant phylogenetically. Identical fold patterns can occur in species which are completely different externally and, conversely, specimens which have very similar external form may, when sectioned, reveal profoundly differing internal morphology.

Currently, the four major groupings within the Nerineacea are based upon gross differences in external shape. There are other differences, for example, the Ceritellidae lack folds, but, as there are also foldless genera within the other groups (*Aphanoptyxis*, *Aptyxiella* etc) this is less significant in terms of distinguishing the groups. At the other end of the scale, species are distinguished from each other on the basis of virtually all morphological criteria; overall shape, ornament, whorl concavity, umbilical morphology, subtle differences in fold pattern etc although the morphological range present in an apparently single species (Chapter 3) offers a cautionary note against a "splitting" approach. Species are grouped together in genera on the basis of close morphological similarities eg same fold pattern (though there may be subtle differences in shape or precise positioning of folds), similar overall morphology, umbilical shape etc. There has been some tendency for generic diagnoses to allow different numbers of folds within a genus (eg *Nerinella* - Cossmann's (1896) diagnosis). This is not useful taxonomically and should be strenuously avoided.

There have been several attempts to relate genera in evolutionary terms (Berthou and Termier, 1972; Rahman, 1967) but few general attempts to draw genera together in subfamily groupings, although Pchelintsev (1968) is a spectacular exception. This reluctance to link genera appears to arise from a lack of any obvious criteria upon which associations should be based; major groupings rely on gross form, species and generic boundaries are drawn on more subtle differences in external and internal morphology,

but the delineation of suprageneric groups remains problematic. The choices include overall shape, presence (and width) or absence of an umbilicus, fold pattern etc. The first two characters are to some extent linked, but the latter appears to be independent. However, fold patterns are not random; trends can be detected which demonstrate that only certain patterns occur, of which a small number predominate throughout the Nerineacea.

### 5.3.2 Fold Patterns

Tables 5.1 and 5.2 show the occurrence of different fold patterns in different genera. Table 5.1 is based on data listed by Cox (ms circa 1953), which are the most comprehensive modern Western European data available; for comparison, the data in Table 5.2 are derived from Pchelintsev's (1968) major review of the group. Some of the genera occur in both tables, even within the same fold grouping, but not very many. This serves to demonstrate the dichotomy which has developed in approaches to nerineid taxonomy.

Both tables show that the vast majority of nerineid genera fall into four main fold categories:-

Fold Pattern	Cox	Pchelintsev
0,0,0,0	19%	25%
1,1,0,0	6%	8%
1,1,1,0	31%	39%
2,1,1(2),0	19%	20%
<b>Totals</b>	<b>75%</b>	<b>92%</b>

These fold categories tend to occur in all the major groupings of the Nerineacea (the Ceritellidae are, of course, represented only by 0,0,0,0) Most of the remaining

KEY FOR BOTH TABLES (5.1 AND 5.2):-

- N - Nerineidae
- I - Itieriidae
- Nl - Nerinellidae
- C - Ceritellidae

TABLE 5.1 COX'S GENERA GROUPED BY FOLD NUMBER

1,1,1,0	N <i>Eunerinea</i> Cox	2,1,1(2),0	N <i>Nerinea</i> ss
	N <i>Acrostylus</i> Cossmann		N <i>Ptygmatis</i> Sharpe
	N <i>Carinia</i> Cox		N <i>Pleisoptygmatiss</i> Böse
	N <i>Eparciella</i> Cox		N <i>Laevinerinea</i> Dietrich
	N <i>Fibuloptyxiss</i> Cox		N <i>Polyptyxis</i> Pchelintsev
	N <i>Melanioptyxiss</i>		I <i>Endoplocuss</i> Cox
	N <i>Melanioplocuss</i> Cox		Nl <i>Bactroptyxis</i> <sup>1</sup> Cossmann
	N <i>Endiatrachelus</i> Cossmann		
	N <i>Adiozoptyxiss</i> Dietrich	0,0,0,0	N <i>Aphanoptyxiss</i> Cossmann
	I <i>Phaneroptyxis</i> Cossmann		I <i>Endiaplocuss</i> Cossmann
	Nl <i>Nerinella</i> <sup>1</sup> Sharpe		Nl <i>Aptyxiella</i> <sup>1</sup> Fischer
			C <i>Pseudonerinea</i> de Lorient
1,1,0,0	N <i>Diptyxiss</i> Oppenheim		C <i>Ceritella</i> Morris and Lycett
	N <i>Julesia</i> Cox		C <i>Fibula</i> Piette
			C <i>Sequania</i> Cossmann

<sup>1</sup>Cox did not recognise a Nerinellidae grouping, so all the above assigned to this group have been assigned to this author.



1,0,0,0	N <i>Monoptyx</i> Cox		
	I <i>Campichia</i> Cossmann	0,1,0,0	N <i>Monoplocus</i> Cox
	I <i>Venedia</i> Mazeran (= <i>Itruvia</i> )		N <i>Trochalia</i> Sharpe
1,0,1,0	N <i>Cossmannea</i> Pchelintsev	0,0,1,0	N <i>Nailsworthia</i> Cox
	N <i>Trochaliopsis</i>		
		3,0,0,0	I <i>Brouzetia</i> Cossmann

**TABLE 5.2 PCHELINTSEV'S GENERA GROUPED BY FOLD NUMBER**

1,1,1,0	N <i>Nerinea</i> Defrance	2,1,1(2),0	N <i>Fibuloptygmat</i> Pchelintsev
	N <i>Acrostylus</i> Cossmann		N <i>Ptygmatis</i> Sharpe
	N <i>Sculpturea</i> Pchelintsev		N <i>Trochoptygmatis</i> Pchelintsev
	N <i>Salinea</i> Pchelintsev		N <i>Scalaeptygmatis</i> Pchelintsev
	N <i>Archimede</i> Pchelintsev		I <i>Pentaptyxis</i> Pchelintsev
	N <i>Etallonea</i> Pchelintsev		I <i>Tetraptyxis</i> Pchelintsev
	N <i>Umbonea</i> Pchelintsev		Nl <i>Bactroptyxis</i> Cossmann
	N <i>Neoptyx</i> Pchelintsev		Nl <i>Polyptyxis</i> <sup>1</sup> Pchelintsev
	N <i>Dioxoptyx</i> Cossmann		Nl <i>Polyptyxisella</i> <sup>1</sup> Pchelintsev
	I <i>Phaneroptyxis</i> Cossmann		Nl <i>Multiptyxis</i> <sup>1</sup> Pchelintsev
	Nl <i>Elatioriella</i> Pchelintsev		
	Nl <i>Elegantella</i> <sup>1</sup> Pchelintsev	0,0,0,0	N <i>Aphanoptyx</i> Cossmann
	Nl <i>Auroraella</i> <sup>1</sup> Pchelintsev		N <i>Endiaplocus</i> Cossmann
	Nl <i>Endiatrachelus</i> <sup>1</sup> Cossmann		Nl <i>Aptyxiella</i> Fischer

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<sup>1</sup>The original major grouping assigned by Pchelintsev is followed here, but the placing of the genus is questionable

	Nl <i>Florella</i> <sup>1</sup> Pchelintsev		Nl <i>Contortella</i> <sup>1</sup> Pchelintsev
	Nl <i>Upella</i> <sup>1</sup> Pchelintsev		Nl <i>Crimella</i> Pchelintsev
	Nl <i>Triptyxis</i> <sup>1</sup> Pchelintsev		Nl <i>Aplocus</i> <sup>1</sup> Pchelintsev
	Nl <i>Nerinella</i> Sharpe		Nl <i>Valanginella</i> <sup>1</sup> Pchelintsev
	C <i>Melaniptyxis</i> <sup>1</sup> Cossmann		Nl <i>Tauricella</i> <sup>1</sup> Pchelintsev
	C <i>Fibuloptryxis</i> <sup>1</sup> Cossmann		
		0,1,0,0	N <i>Cryptoplocus</i> Pictet and Campiche
1,1,0,0	N <i>Turbinea</i> Pchelintsev		N <i>Conoplocus</i> Pchelintsev
	N <i>Diptyxis</i> Oppenheim		
	N <i>Cylindroptyxis</i> Pchelintsev	1,0,1,0	N <i>Cossmannea</i> Pchelintsev
	I <i>Campichia</i> Cossmann		I <i>Itieria</i> Matheron
1,0,0,0	N <i>Funiptryxis</i> Pchelintsev		

25% (Cox) or 8% (Pchelintsev) fall into four fold categories, all of which are simple arrangements of one or two folds; there are two further categories with only one genus in each.

In most cases, the broad fold category is directly comparable in different genera; the basic fold pattern is the same, and the folds are also similarly placed on the whorl walls. There may be minor differences, for example, with the additional presence of small folds increasing the overall fold number, for example in the category 2,1,1(2), 0, where a small second labral fold is sometimes present, a basal fold also arises in some genera. These "additional" folds are usually insignificant compared to the major folds present, and are considered to have minimal significance in terms of evolutionary trends. The same consideration applies to genera that develop complex bifurcating folds. These complex folds invariably develop from simpler folds with increasing distance from the aperture (figure 4.2). The basic pattern can be the same in both simply and complexly folded genera, but in the latter, it seems that carbonate deposition has continued to give more elaborate structures. This is not thought to be of major phylogenetic significance.

There appear to be several basic fold patterns which occur throughout the Nerineacea and seem to represent "stable" configurations. From an evolutionary standpoint, there are two basic options:-

- 1 the stable fold patterns evolved once, and were then "carried through" into widely differing morphological groups
- 2 the stable fold patterns developed independently with the major morphological groups

The second option is thought to be considerably more likely; there is a distinct lack of repeated intermediate forms linking the major morphological groupings, in addition, it is considerably easier to envisage change occurring by the development or loss of folds rather than as major reorganisation of overall shell morphology. It is therefore

concluded that stable fold configurations evolved repeatedly within the major nerineacean groups.

These stable patterns most probably reflected anatomical features of the nerineid animal. The functional significance of the folds is not clear (Section 4.3) but they must have been in intimate contact with the digestive gland of the snail throughout most of the shell length. Conceivably the folds reflected invaginations of the digestive gland, or areas where the fold protruberances would not affect the functioning of the gland. The fact that these stable folds patterns are not widespread in other multifolded groups such as the Campanilidae (Delpey, 1941) implies that the anatomical relationship which existed between the folds and soft tissue were not comparable to those occurring in the Nerineacea.

If the stable patterns are considered within a single nerineacean grouping (eg the Nerineidae) there are again two options concerning their evolution:-

- 1 stable fold patterns evolved repeatedly within the group
- 2 stable fold patterns evolved only once, and diversification of other morphological features then occurred

At present it is not clear which of these occurred, but it is extremely important that future work considers the problem. The author considers that 2 is more likely, but acknowledges that further study is required to establish the principle. The possible use of cladistics is severely hampered by both the limited number of characteristics which are available, and the fact that the "primitiveness" of specific nerineid characters are not clear.

If 2 is accepted, then lineages within the major groupings would be based on similarity of fold number, linking genera such as *Eunerinea* and *Pchelinsevia* together and separating them from groups such as *Ptygmatis*, *Plesioptygmatis*, and *Laevinerinea* which would be considered to represent a separate phylogenetic branch. Suggestions

such as Akopyan (1973) which derive *Plesioptygmatis* from "*Diozoptyxis*" (= *Pchelinsevia*) could not be accepted. The issue is not easy to resolve; if fold number is used, it is perhaps relatively easy to envisage the connection between *Eunerinea* and *Pchelinsevia*, with the latter developing an umbilicus and correspondingly more conical shell; external whorl shape and ornament is similar in both groups. However, if this argument is followed, then *Endiutrachelus* must also be linked; although in overall shape it is elongate and cylindrical, and therefore similar to *Eunerinea*, it has a very different whorl profile (convex with a slight depression at the suture) and completely lacks ornament. It is essential to resolve the issue if a suprageneric classification is truly to reflect phylogenetic relationships.

#### 5.4 CONCLUSIONS

The nerineids were an exclusively Mesozoic group that appeared around the Triassic/Jurassic boundary, and became completely extinct by the end of the Cretaceous. The extinction episodes that the group suffered can be related to rapid environmental changes connected with changes in sea level. The main extinction episode for the group occurred between the Late Cenomanian and Early Coniacian, and coincides with two major extinction events (Cenomanian/Turonian and Turonian/Coniacian, Kauffman, 1984) that affected many other groups. By comparison with this event, the final extinction of the group at the end of the Cretaceous was relatively insignificant in terms of extinction rate, involving only two or possibly three remnant genera which seem to have been restricted to refuge areas in the Caribbean. The terminal event can also be related to rapid sea level fluctuation. It is possible that the Campanilidae to some extent succeeded the nerineids ecologically.

The Nerineacea can be split into four major groupings which are based largely on gross morphology. Within these groups, a limited number of fold configurations occur. These seem to represent stable fold patterns that conformed to anatomical features of the

nerineacean animal. The stable fold patterns appear to have arisen independently in most of the major groups. It is considered probable that, within a single major group, genera with the same fold patterns are more closely related than those with differing fold patterns, but this is not proven. It is important, however, that the issue is resolved as it has profound implications for suprageneric evolutionary relationships.

## CHAPTER 6

### THE SYSTEMATIC AFFINITIES OF THE NERINEACEA

#### 6.1 INTRODUCTION

Subdivision of the Gastropoda is largely neontologically based, using various anatomical features of extant groups. Palaeontologists in general accept the resulting subdivisions of the class and attempt to place fossil groups within them on the basis either of direct or indirect relationships with extant snails, or inferences concerning soft tissue characteristics based on shell morphology. Both of these approaches have been used with respect to the Nerineacea but the position of the group within higher gastropod taxonomy has remained debatable.

A number of factors have added to the difficulties involved in attempting to place the nerineids. The group became extinct during the Upper Cretaceous and there are no obvious descendants either in the Tertiary or extant today. The Nerineacea are rather sharply delineated from other gastropods by a number of characters (see page 1) and cannot readily be related to any directly ancestral taxa. In particular it has proved difficult to find characters homologous to the juxtasutural slit, selenizone and internal folds. The wide morphological diversity which occurs within the Nerineacea has further complicated the issue, particularly in respect of the striking superficial similarities which exist between some nerineid groups and various other gastropods (eg the Itieriidae and Acteonellidae; *Cryptoplocus* and Campanilidae).

The approach of most workers has been to try to relate the nerineids to other gastropod groups which possess one or more characters perceived as homologous to those occurring in the Nerineacea. The nerineids have then been placed close to or within the "related" group, and have thus derived their position in the Gastropoda. A few workers (Djalilov, 1975; Barker, 1976) have, mainly on the basis of apertural

morphology, made suggestions concerning the probable anatomy of the nerineid animal which have then been used to place the group.

Different workers have put the Nerineacea in the Archaeogastropoda, Mesogastropoda, Neogastropoda and Opisthobranchia without any general consensus emerging. The approaches and conclusions which have resulted in these various placings will now be considered.

## 6.2 PROPOSED AFFINITIES

### PROSOBRANCHIA

#### 6.2.1 Archaeogastropoda

On the basis of a common sinus and selenizone, Böhm (1900) related the Nerineidae to the Murchisoniidae, arguing that the internal folds of the nerineids had caused the sinus to move posteriorly from its anterior/median position in the Murchisoniidae. This suggestion is highly improbable as the folds in nerineids are not present until at least half a whorl back from the aperture, and can therefore have little or no direct effect on apertural morphology.

Delpy (1939) postulated the Nerineacea may have originated from elongate Pleurotomariidae<sup>1</sup>, although she apparently considered the Nerineidae to be close to the Opisthobranchia and the Neogastropoda (see p 216).

Pchelintsev (1968) rejected any association between the nerineids and the opisthobranchs, maintaining that the group had originated from various branches within the Murchisoniidae. He argued that a direct succession in terms of general shell type and apertural shape existed between the Palaeozoic and Mesozoic families, and

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<sup>1</sup>"Les Nerineidae ..... semblent provenir de Pleurotomariidae élanés" Delpy, 1939, p 23 (The Nerineidae ..... seem to come from elongate Pleurotomariidae).



also that phylogenetic affinities clearly existed between each nerineid family and various sections within the Palaeozoic Murchisoniidae (see section 1.3.8). Pchelintsev's suggestions imply a polyphyletic origin for individual nerineacean families, deriving them from various Murchisoniidae branches, some in the Cambrian, others in the Permian. These proposals concerning the systematic derivation and affinities of the Nerineacea are not generally accepted.

Djalilov (1975) considered that profound morphological differences such as apertural shape, internal folds and sutural ramps distinguished the Nerineacea from the Murchisoniidae, and also that the posterior juxtasutural position of the sinus in the former reflected gross differences in anatomy from that which existed in the Murchisoniidae where the slit was medially placed. The latter argument is perhaps the most convincing, and the author supports Djalilov's total rejection of any relationship between the two groups.

#### 6.2.2 Mesogastropoda

The genus "Nerinée" was related by many earlier workers to the "cérites" (Defrance, 1824; Blainville, 1827; Deshayes, 1827; Rang, 1829; Deslongchamps, 1842). This association was based upon a common turreted morphology, similar aperture shape, particularly in respect of the anterior siphonal canal, and also the occurrence of internal folds in some "cérites".

Zittel (1873) placed the newly erected Nerineidae as an independent family between the "Cerithiden" and the "Pyramidelliden". De Trilobet (1874) considered the "columella canal" of the nerineids paralleled that of the "Buccinides" and "Cérithides" and Martin (1889) described parietal and basal folds in *Telescopium fuscum* Chemnitz which he considered to be similar to nerineid folds. Martin acknowledged that *Telescopium* lacked the posterior sinus characteristic of the nerineids, but pointed out that such a sinus, albeit in a slightly different position (separated from the suture by a row of tubercles), was present in another cerithiid genus *Vicarya*; indeed Böhm (1900)

suggested that the Tertiary genus *Vicarya* was a descendant of the Nerineidae. On the basis of this evidence, Martin suggested a close relationship existed between the nerineids and *Cerithium*.

Delpey (1941) considered that the Tertiary Campanilidae, usually considered to belong in the Cerithiacea (Houbrick, 1981), were descendants of the Nerineacea. Houbrick (1981) stated that this was most unlikely because of the reported heterostrophic protoconch of the Nerineacea, and also the posterior slit. He considered that any similarities between the two groups were due to convergence.

Yochelson (1956) while describing a new Permian subulitid<sup>1</sup> genus *Labridens* noted that the latter possessed internal folds on the columella and labral wall which became emplaced a short distance behind the aperture, and that the aperture was terminated abapically by a siphonal notch. The similarity of these features to those occurring in some Nerineacea caused Yochelson to suggest that a relationship between the two might exist, although he acknowledged that the evidence was inconclusive.

Djalilov (1975) maintained that the possession of a siphonal canal and anal notch were sufficient grounds for the placement of the nerineids in the "monobranchial prosobranchs"; he noted that a heterostrophic protoconch had been reported in only one atypical genus - *Pseudonerinea*.

Barker (1976) suggested that the posterior position of the slit in the Nerineacea, as opposed to the median/anterior position in the Pleurotomariacea and Murchisoniidae indicated the development of asymmetry in the former group, which, when combined with the presence of a siphonal canal, indicated that the Nerineacea were a primitive caenogastropod family which had retained some archaeogastropod characteristics.

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<sup>1</sup>The placing of the Subulitacea in the Mesogastropoda here follows Taylor and Sohl (1962).

### 6.2.3 Neogastropoda

A small number of workers have suggested that the nerineids were neogastropods; Delpy (1939) stated "les Nerineidae et les Orthostomidae soient suffisamment proches pour raccorder les Opisthobranchiata et les Prosobranchiata Stenoglossa Toxoglossa" (p 23) (the Nerineidae and the Orthostomidae are sufficiently close to connect the Opisthobranchiata and the Prosobranchiata Stenoglossa Toxoglossa).

Knight (reported in Cox ms circa 1953), on the basis of a common juxtasutural posterior slit, related the Nerineacea to the Conidae, and argued that the former were early neogastropods.

## OPISTHOBRANCHIA

### 6.2.4 Pyramidellacea

Some of the earliest workers suggested an association between *Nerinea* and the "pyramidelles" (Defrance, 1825; Pusch (reported in Bronn, 1836)). D'Orbigny (1843) considered that the internal folds, turriculate shape and often open umbilici of *Nerinea* species demonstrated a close relationship with the "pyramidelles" although the discontinuous nature of the folds and the lack of a proper sinus in the latter group were acknowledged.

Pictet and Campiche (1862) also placed the "Nerinees" in the "Pyramidellides" family, but noted that the genus appeared to be linked on the one hand to the "cérites" by *Cryptoplocus* and on the other to the "Acteonelles" by *Itieria*. However, Stoliczka (1867) saw great similarities between *Itieria* and *Obeliscus*; *Cryptoplocus* and *Niso*; *Nerinea* and *Pyramidella*; he therefore considered that the nerineids definitely belonged within the Pyramidellidae. De Trilobet (1874) suggested that in apertural morphology *Nerinea* most closely approached the "Pyramidellides", although other features appeared to link the group to other families.

Cossmann (1921) considered that the common features of heterostrophy in the earliest whorls and columella plication linked the Entomotaeniata and Pyramidellidae; he postulated that the pyramidellids were descended from the "opisthobranchs" via the nerineids.

Wenz (1940) associated the Nerineacea with the Pyramidellacea and the opisthobranchs, but was equivocal as to whether the nerineids were closely allied to the pyramidellids or formed an independent group.

Taylor and Sohl (1962) included the Nerineacea as a superfamily together with the Pyramidellacea in the order Entomotaeniata within the Euthyneura.

#### 6.2.5 Acteonacea

Cossmann (1895a and 1895b) related first the Ceritellidae (= "Tubiferidae") family to the Acteonidae and later (1896) whole suborder Entomotaeniata (comprising the Ceritellidae, Nerineidae and Itieriidae) to the "Tectibranchs" on the basis of a common heterostrophic protoconch (although this had only been reported in the Ceritellidae, see figure 6.5a and b) and a "complete sequence" linking the Acteonidae to the Nerineidae. He also considered that both a posterior juxtasutural sinus and an abapical siphonal canal could be demonstrated in some Acteonidae. Cossmann concluded that the organisation of the nerineid animal had probably been intermediate between prosobranch and opisthobranch, with somewhat greater affinities to the latter.

Dietrich (1925) rejected Cossmann's unification of the Ceritellidae, Itieriidae and Nerineidae in the Entomotaeniata, and considered that as a heterostrophic protoconch had been reported only in the Ceritellidae, there was no evidence to support the association of the Itieriidae and Nerineidae with the Acteonellidae and opisthobranchs. This view was supported by Djalilov (1975). Barker (1976) considered that the heterostrophic protoconch in the Ceritellidae was so poorly documented that its actual existence was questionable. However, Kollmann (1967) accepted Cossmann's observations and argued that the combination of a heterostrophic protoconch and an

anal sinus was unlikely to have evolved twice, and therefore suggested that the Acteonellidae and Nerineacea were both descended from the Acteonidae.

#### 6.2.6 Incertae Sedis

Cox (1958) pointed out that the Ceritellidae and Itieriidae had a general opisthobranch appearance and that the Ceritellidae at least appeared to have had a heterostrophic protoconch. However, he also indicated that the anterior siphonal canal and the posterior sinus were non-opisthobranch features and suggested that, as the nature of the protoconch in the Nerineidae and Itieriidae was not known, the Nerineacea should be regarded as a distinct suborder of uncertain affinities.

#### 6.2.7 Delpey's Subdivision of the Gastropoda

In an attempt to subdivide the gastropods (excluding the Pulmonata) solely on the basis of shell character, Delpey (1939 and 1941) set up three sections based on growth line pattern. Delpey (1941, p14) states "Les traces extérieures des lamelles sur la surface de la couche externe constituent les stries d'accroissement. Elles sont donc modifiées par les changements produits à l'intérieur de la cavité palléale, en particulier par les modifications branchiales" (The external traces of the lamellae on the external surface constitute growth lines. They are therefore modified by the changes occurring in the interior of the pallial cavity, in particular by branchial modifications). Cox (1958, p 248) notes "the scheme is based on the theory that the inclination and curve of the outer lip of the aperture..... were relatively stable in long lines of gastropod descent and are therefore a good basis for phylogenetic classification". Delpey's Group III consists of gastropods with opisthocline growth lines, and includes the "Nerineidae, Campanilidae, Pleurotomidae, Conidae and Actaeonidae" (Delpey, 1941, plate 3).

This classification does not conform to neontologically based taxonomy and has not been adopted to any significant degree by later workers.

### 6.2.8 Discussion

It is clear from the above review that the Nerineacea have proved extremely difficult to place satisfactorily within the Gastropoda. The problems encountered when attempting to reconstruct anatomical characters from shell morphology alone are quite formidable, and approaches based on homological arguments have not clarified the issue. The present situation regarding the systematic position of the Nerineacea is exemplified by the treatment of the group in museum collections. The British Museum (Natural History) houses the nerineids alongside the primitive opisthobranchs, at the Musée d'Histoire Naturelle in Paris, there is an exhibition covering the affinities between the Nerineacea and Cerithiacea whereas the Musée Geologique at Laussane includes the group among the neogastropods.

The present situation of the Nerineacea is therefore problematical. However, new evidence outlined in the following section indicates a more definitive placing of the group.

## 6.3 NEW EVIDENCE

### 6.3.1 Material and Approach

Recent re-examination of material in the British Museum (Natural History) Collection has revealed specimens of two Nerineacea species with intact protoconchs. The descriptions of these species and details of the specimens involved are given in Chapter 2 (sections 2.17 and 2.27.1). The species concerned are *Polyptyxisella schicki* (Fraas) (BM(NH) G3809<sup>1</sup>), belonging to the Nerinellidae, and *Diozoptyx cochleaeformis* (Conrad) (BM(NH) G17262<sup>1</sup>) which is placed within the Nerineidae.

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<sup>1</sup>Locality and stratigraphic details are given in the appropriate section of Chapter 2.

These protoconchs were studied using both a light microscope (a Wild Heerbrugg M8 Stereo Microscope), up to x50 magnification and a scanning electron microscope (SEM, a Cambridge Stereoscan 600 and an ISI 60 A) using up to x 500 magnification. Although preservation is not perfect, the basic features of the protoconchs are clearly visible.

### 6.3.2 Results

The protoconch of ?*P. schicki* is deviated, paucispiral and heterostrophic. It consists of approximately one whorl with an axis of coiling deviated by approximately 90° from that of the teleoconch. The direction of coiling, when viewed from the extreme apex of the shell (see figure 6.1d), is in an anticlockwise direction.

Both the protoconch and the early teleoconch whorls are smooth and there is no distinct junction visible between the two, apart from the change in coiling axis, although a slight discontinuity (arrowed in figure 6.3a and e) may represent the contact point. The teleoconch coils in a clockwise direction. The dimensions seem to be reasonably constant in all specimens studied and are given in figure 6.2A.

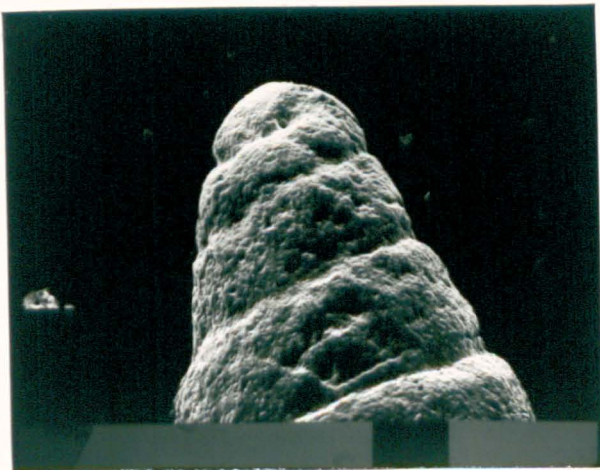


Figure 6.1 SEM micrograph of the protoconch of ?*P. schicki*.

Orientation is similar to that in figure 6.1A.

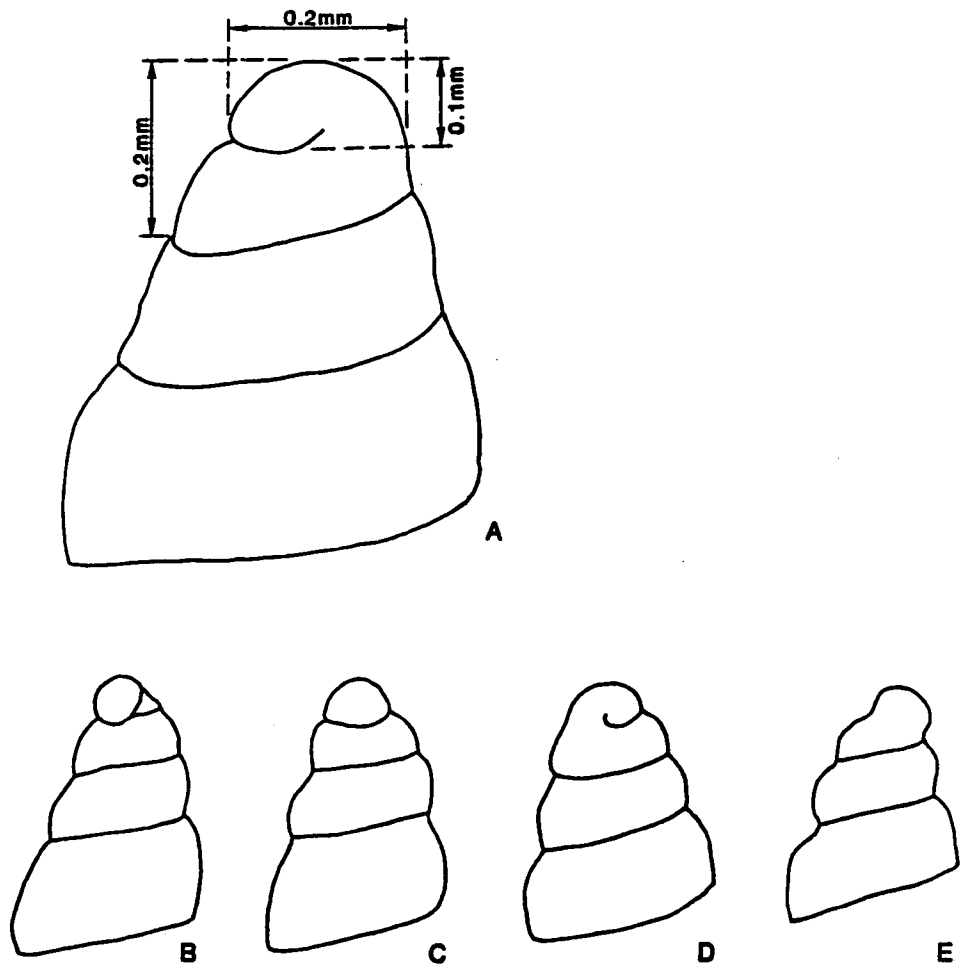


Figure 6.2 Camera lucida drawings of the protoconch of *P. schicki* (Fraas).  
BM(NH) G3809.

A - approximate dimensions of the protoconch

B - E views of the protoconch as the shell is rotated from the position in A towards the observer's right. Between C,D ,E and A there is a total rotation of  $360^\circ$ , with a rotation of about  $90^\circ$  between each figure.

D - the heterostrophic nature of the protoconch is shown in this view



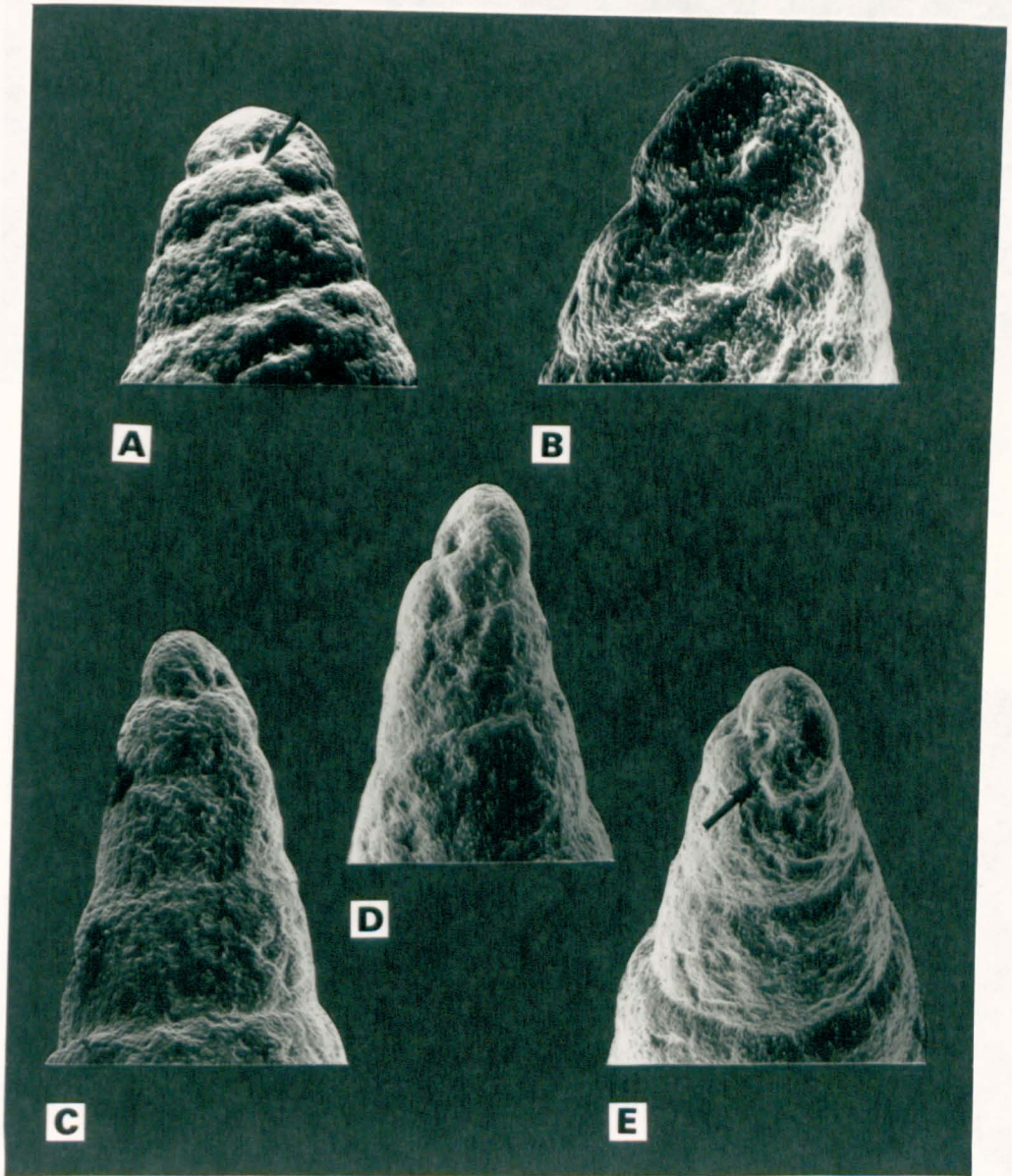


Figure 6.3a,b,c,d,e SEM micrographs showing various views of the protoconch of *P. schicki* at x 100 (a,c,d,e) and x 200 (b) magnifications (for scale see 6.1a).

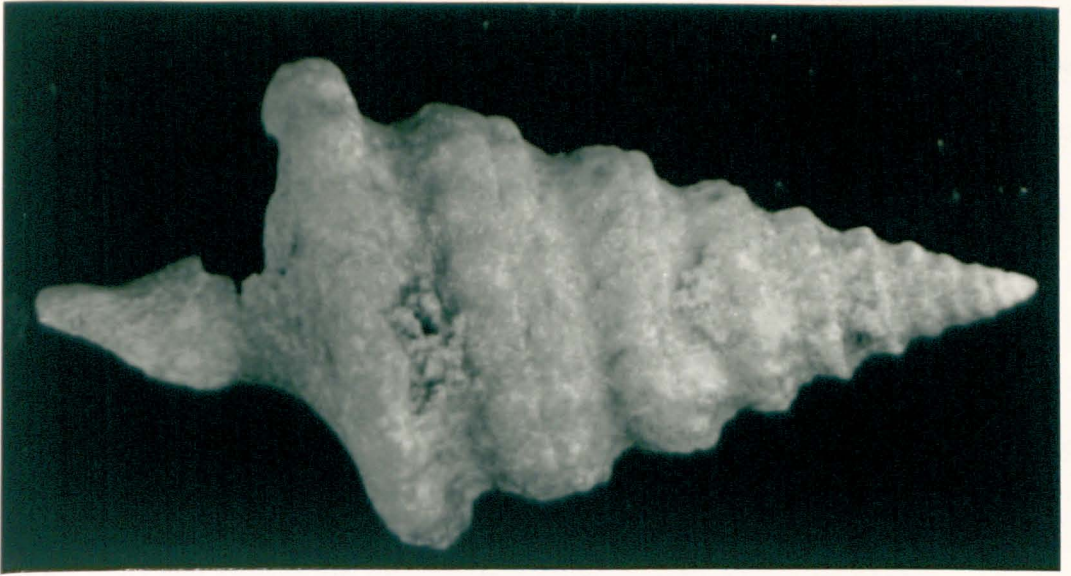


Figure 6.4a The *D. cochleaeformis* shell which has its protoconch preserved. BM(NH) G17262.

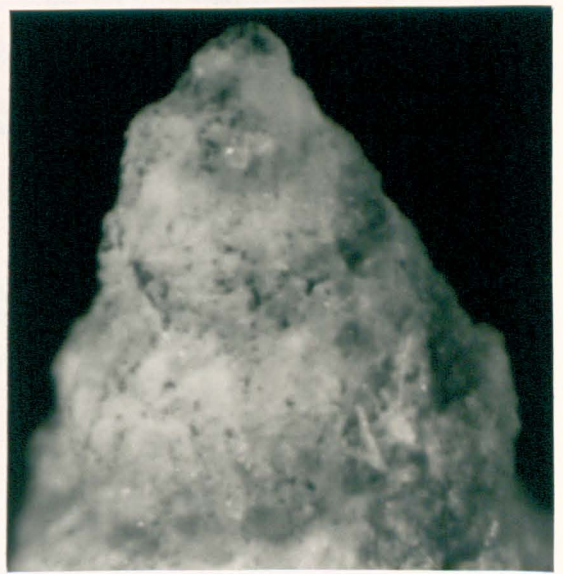


Figure 6.4b,c Two views of the protoconch of *D. cochleaeformis* taken under the light microscope at x 50 magnification. The dimensions are almost identical to those given in 6.1a.

Only one specimen of *D. cochleaeformis* is available with the protoconch preserved, and this is somewhat eroded (figures 6.4b and c). However, the overall orientation, coiling and shape appears to be very similar to that of ?*P. schicki* and the dimensions are almost identical.

### 6.3.3 Discussion

This is the first time that the protoconchs of any Nerineidae or Nerinellidae species have been described. The nature of these embryonic whorls have important implications for the unity and affinities of the Nerineacea as a whole.

The occurrence of virtually identical protoconchs in two very different genera, belonging to different families, implies that these were a common feature occurring throughout the Nerineidae. The similarity between these protoconchs and those reported in the Ceritellidae by Cossmann (1895, *Ceritella carinella* Buvier) and Bigot (1896, *Pseudonerinea clio* (d'Orbigny)) is readily apparent (compare figures 6.5a and b with 6.1a, b, c and d and 6.3 a,b,c and d).



Figure 6.5a Cossmann's (1895) figure of the protoconch of *Ceritella carinella* Buvier.

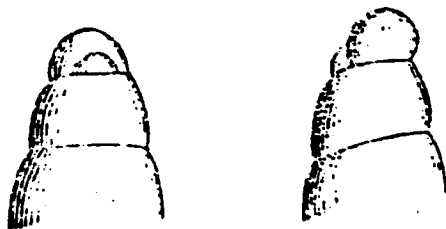


Figure 6.5b Bigot's (1896) two figures of the protoconch of *Pseudonerinea clio* (d'Orbigny).



The discovery of these protoconchs has two major implications. Firstly, they provide further confirmation of the systematic unity of the Entomotaeniata, first suggested by Cossmann (1896) but later criticised because a heterostrophic protoconch (one of Cossmann's major unifying characters for the group) had been reported only from the Ceritellidae (Dietrich, 1925). Heterostrophic protoconchs are now known from at least three of the four nerineid families<sup>1</sup>. Secondly, the widespread occurrence of heterostrophic protoconchs throughout the group means that any systematic affinities proposed for the Nerineacea must account for these. Previously the occurrence of heterostrophic protoconchs in the Ceritellidae tended to be disregarded either as a poorly defined feature, the existence of which was not proven (Barker, 1976) or as merely a feature of an aberrant group (Djalilov, 1975).

Heterostrophic protoconchs are characteristic of opisthobranchs (Cox, 1960), but may not be confined exclusively to this subclass. Both the Architectoniacea and the Mathildidae (the latter is sometimes included in the superfamily Cerithiacea) have heterostrophic protoconches and both have been generally placed in the Mesogastropoda. However, in the case of the Architectoniacea, the heterostrophic protoconch is submerged, its direction of growth having been exactly opposite to that of the teleoconch. Thus the nature of the Architectoniacea protoconch is very different from that seen in the Nerineacea. In the Mathildidae the protoconch appears quite similar to that seen in the Nerineidae, although it is multispiral with a number of tightly

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<sup>1</sup>Cossmann (1921, p 209) stated "des coquilles nerineiformes (*Itieria* et surtout *Itruvia*) dont la plication columellaire et la protoconque heterostrophe" (some nerineid-shape shells (*Itieria* and especially *Itruvia*) with columella folds and a heterostrophic protoconch), which Knight et al (1960) have interpreted as a statement that *Itruvia* (family Itieriidae) possessed a heterostrophic protoconch. The present author has been unable to locate any description or figure of an itieriid protoconch, either by Cossmann or any other worker, which, when taken together with the ambiguity in Cossmann's statement, would seem to indicate that the protoconch in the Itieriidae is not known.

coiled whorls within the deviated apex, a feature which does not occur in the nerineid protoconchs described above.

The positioning of the both of the above groups within the Mesogastropoda has recently been questioned, and a new group, the Heterogastropoda, has been proposed to accommodate groups which appear to be intermediate between prosobranch and opisthobranch organisation (Fretter and Graham, 1982). It has been suggested that the Mathildidae were primitive opisthobranchs (Taylor and Sohl, 1962) and Knight et al (1960) included the family in the Pyramidellacea. There does not appear to be any additional evidence to link the Nerineacea to these "mesogastropod" groups with heterostrophic protoconchs, although Bouchet (pers comm) reports a rare deep sea Mathildidae genus, *Gegania*, which has a posterior slit, although no slit band results from this.

Among the more primitive shell-bearing opisthobranchs, protoconchs are usually (but not exclusively) heterostrophic (Knight et al, 1960) and some appear to be very similar to those of the Nerineacea. The protoconch occurring in *Acteonina* is almost identical to that found in the nerineaceans apart from very slight differences in dimensions. The protoconch of *Turbonilla* (Pyramidellacea) (Knight et al, 1960) also appears to be similar.

The heterostrophic protoconch of the Nerineacea therefore strongly indicates opisthobranch affinities.

#### 6.4 ESSENTIAL CONSIDERATIONS FOR A SYSTEMATIC PLACEMENT

A number of characters and features must be considered when attempting to place the Nerineacea. These are :-

- 1) the rudimentary abapical siphonal canal, present to a greater or lesser degree in all nerineids

- 2) the juxtasutural selenizone, from which the presence of a posterior slit is inferred at the aperture in all nerineids. Associated with this is the occurrence of opisthocline growth lines throughout the group
- 3) a heterostrophic protoconch occurring in at least three of the four families (Ceritellidae, Nerineidae and Nerinellidae)
- 4) very distinctive internal folds in many, but not all, genera
- 5) aragonitic cross-lamellar shell structure
- 6) wide range of shell shapes included within the Nerineacea

## **6.5 DISCUSSION OF SYSTEMATIC AFFINITIES**

If the systematic unity of the four families Ceritellidae, Itieriidae Nerineidae and Nerinellidae are accepted, then the relevance of several of the above characters, when considering a taxonomic placing of the group, becomes negligible.

The extremely wide morphological diversity within the superfamily precludes the use of overall morphology when attempting to relate the group. Such an approach would merely result in the fragmentation of the superfamily, with various genera being associated with different groups throughout the Gastropoda. The only possibility of using such an approach successfully would be with respect to the morphology of the earliest nerineids from the Lower Jurassic while attempting to identify a likely ancestor for the group. This study has concentrated almost exclusively on Cretaceous material, and therefore such an approach is beyond the scope of this work.

The cross-lamellar aragonitic shell structure, which has been reported in various Upper Cretaceous nerineid species (Barker, 1976) is a common microstructure in the Gastropoda, and does not enable any deduction concerning the systematic affinities of nerineids to be made.

Internal folds, although a distinctive feature, do not occur in all Nerineacea. The ceritellids lack folds altogether, as do certain Nerineidae and Nerinellidae genera such as *Aphanoptyx* and *Aptyxiella*, which in all other respects are typical of their respective families. In addition, Barker (1976) noted that although internal folds occur in many different gastropod groups, the nature of such folds are very different from those occurring in the Nerineacea (see section 4.3). Barker stated that only two groups showed fold morphologies comparable to those found in the Nerineacea, the Permian subulitid *Labridens* Yochelson, and the Jurassic zygopleurid *Rigauxia* Cossmann. He concluded that any similarity between the fold morphologies of these two genera and those of the Nerineacea were merely the result of homeomorphic evolution.

There are therefore essentially three characters at least two of which appear to be universal among the Nerineacea, which seem to be of direct relevance when considering the affinities of the group. These are the anterior canal, posterior slit (together with the associated opisthocline growth lines) and heterostrophic protoconch.

Cox and Knight (1960) noted that some Murchisoniacea had an incipient abapical canal, and the posterior slit and juxtasutural slit band have been homologised with the medially placed slit of the Murchisoniacea (Böhm, 1900; Pchelintsev, 1968), thereby connecting the Nerineacea with the Archaeogastropoda. However, the slit and slit band, although structurally equivalent in the two groups, are in markedly different positions which must reflect profound changes in soft part morphology (Djalilov, 1975). This difference, together with the occurrence of heterostrophic protoconchs in the Nerineacea precludes the possibility of any close phylogenetic affinities existing between the two groups.

The nerineids have long been associated with the Cerithiacea, and hence the mesogastropods. The evidence used to support this association includes a similar abapical siphonal canal in both groups, similar turritelliform shape (although not all nerineids are turritelliform), the occurrence of internal folds in some cerithiids and also the presence of a slit or sinus near the suture in some genera. However, the

morphological diversity with the Nerineacea precludes the use of shell shape as an indicator of taxonomic affinity, and cerithiid internal folds are significantly different from those occurring in nerineids. Some cerithiids show a sinus (eg *Campanile*) or a slit (eg *Vicarya*) in the outer lip, however, these are not actually at the suture, but somewhat abapical to it. The short anterior canal found in the Nerineacea does indeed resemble the siphonal canals occurring in some Cerithiacea, although other caenogastropod groups also have such features, which appear to have evolved repeatedly in unrelated groups (Taylor et al, 1980). The occurrence of heterostrophic protoconchs within the Mesogastropoda now appears questionable (Fretter and Graham, 1982); the groups possessing such protoconchs do not, in any case, show any other features that might link them to the Nerineacea. There does not appear to be any satisfactory evidence for linking the two groups.

The more fundamental approach of both Djalilov (1975) and Barker (1976), based on analysis of nerineid apertural morphology rather than supposed homologous features, concluded that the nerineids were caenogastropods. However, the evidence for a heterostrophic protoconch was ignored (for different reasons - see p 215). The occurrence of such a protoconch is now beyond doubt; any placement of the group must therefore account for this feature. Apertural morphology indicates that the nerineid animal was asymmetrical which precludes a placement in the Archaeogastropoda; it does not, however, exclude the possibility of opisthobranch affinities.

The evidence put forward to link the Nerineacea with the Conidae and thus the Neogastropoda (Knight, reported in Cox ms circa 1953) relies on the common occurrence of a juxtasutural sinus. This is insufficient to link the two groups, particularly as it is found in other gastropods as well eg the Acteonidae (Kollmann, 1967; Barker, 1976). In addition, the occurrence of heterostrophic protoconchs in the Nerineacea does not support such an association.



The association of the Nerineacea with the Pyramidellacea has been based on similar shell morphologies, the presence of heterostrophic protoconchs in both groups and the occurrence of internal folds in some pyramidellids. Shell shape is an unreliable parameter upon which to base proposed affinities, and the folds which occur in some pyramidellids differ significantly in nature from those of the Nerineacea. The heterostrophic protoconch alone does not provide sufficient evidence to associate the two superfamilies as it is a feature found throughout the shelled opisthobranchs.

The Nerineacea have also been associated with the opisthobranchs via the Acteonidae (Cossmann, 1896; Kollmann, 1967) on the basis of a common heterostrophic protoconch (although prior to the present work only reported in the Ceritellidae), a posterior juxtasutural sinus, and an abapical siphonal canal in some Acteonidae. A heterostrophic protoconch has now been confirmed in three nerineid families; the similarity between the protoconchs of *Acteonina* and *Polyptyxisella* is quite striking.

Kollmann (1967) reported a posterior "anal sinus" at the suture in *Trochacteon*, and stated that this was an opisthobranch character; Taylor et al (1980) also note that opisthocline apertures are characteristic of opisthobranchs. Thus the sinus occurring in some Acteonellidae and the slit of the Nerineacea are both in the same position, the difference between the two being merely that of depth in that the shallower sinus of the acteonellids did not generate a slitband when infilled, whereas the deeper slit of the nerineids did. It seems likely that the position of the sinus or slit in the apertural margin is of greater relevance when attempting to homologise the structures than the actual degree of depth involved; Yochelson (1984) while discussing Palaeozoic gastropods stated that a continuous spectrum existed between those with a narrow shallow sinus to those with a distinct slit. Cossmann (1896) stated that an abapical siphonal canal was present in some Acteonidae, and Kollmann (1967) notes that the *Trochacteon* aperture is weakly notched at the base. The Nerineacea Acteonidae and Acteonellidae therefore appear to share, to some extent, the three features considered phylogenetically significant.

## **6.6 SYSTEMATIC PLACEMENT**

The heterostrophic protoconch, opisthocline aperture and posterior juxtasutural slit of the Nerineacea indicate opisthobranch affinities for the group. It appears that the nerineids were primitive opisthobranchs which were probably closest to the Acteonidae and Acteonellidae (Order Cephalaspidea, Superfamily Acteonacea (Taylor and Sohl, 1962). The degree of affinity does not appear to be close, the presence of an anterior canal clearly separates the Nerineacea.

It is proposed that the Nerineacea should be placed in the Opisthobranchia in a separate Order Entomotaeniata (excluding the Pyramidellacea). The Entomotaeniata are considered to show affinities with the Acteonidae and Acteonellidae (Acteonacea) but were quite distinct from these families.

## CHAPTER 7

### CONCLUSIONS

#### 7.1 INTRODUCTION

Despite a promising early start, the Nerineacea have become a severely neglected group, regarded by most workers who encounter them in the course of other research as objects of curiosity value only. A vicious circle arises whereby, since little is known about nerineids, they are perceived to be of no significance; any which are found in the course of non-specialist research tend to be ignored or vaguely noted as "small nerineids" (or similar). The amount of information available about the group is therefore minimised, and thus little is known about them. There is clearly a role in this scenario for specialist workers to step in and publicise aspects of the group which have a useful application in more general study. Unfortunately, the number of nerineid workers is small, and the neglect has been long-term. However, it is hoped the discussion given in earlier chapters covering the palaeoecology, taxonomy and stratigraphic ranges of Cretaceous nerineids will contribute to emphasising the relevance and potential of the Nerineacea. Since nerineids form a significant component of Mesozoic Tethyan shallow marine macrofaunas, their possible contribution, particularly to the correlation of shallow marine carbonates, cannot be ignored.

Historically, nerineids received considerable attention in the middle and latter part of the 19th century, largely from European workers such as d'Orbigny, Sharpe, Coquand, Pictet and Campiche, de Loriol, Stoliczka, Zittel, Cossmann and Choffat who were producing taxonomic catalogues or large monographs on the fauna of Mesozoic carbonate deposits. Although there have been several notable extensive studies of the group published during the 20th century (notably by Dietrich, Delpey and Pchelintsev) these have not resolved systematic difficulties

and have failed to emphasise the wider relevance of the group. The Nerineacea have not previously been subject to a modern palaeontological analysis, with the exception of Barker's (1976) study of Bathonian forms.

## 7.2 AFFINITIES AND TAXONOMY

The Nerineacea have, at various times, been associated with every major gastropod division apart from the Pulmonata. The systematic affinities of the group have remained unclear. The evidence presented here describing the heterostrophic nature of the nerineacean protoconch (here reported in Nerineidae and Nerinellidae species) unequivocally indicates opithobranch affinities. The Nerineacea are considered to be primitive Opisthobranchia which were most closely allied to the Acteonidae and Acteonellidae. They are regarded as sufficiently distinct from these families to merit a separate order, the Entomotaeniata. Previous suggestions which closely associated the Nerineacea and Pyramidellacea, placing both in the Entomotaeniata, do not appear to be well-founded. This proposed relationship is therefore rejected, and the Pyramidellacea are considered to belong to a separate order.

It is interesting to note that the views expressed here on the taxonomic affinities of the Nerineacea are almost entirely in accordance with those first expressed by Cossmann (1896) when he erected the Entomotaeniata.

The Nerineacea are divided, on the basis of gross morphology into four families, the Ceritellidae, Nerineidae, Nerinellidae and Itieriidae. The first three appear to have separated relatively early in the early Jurassic, with the Nerinellidae possibly being the stem group. The Itieriidae diverged from the Nerineidae considerably later; their ovate shape has secondarily evolved to resemble certain Acteonacea.

Within each family (apart from the Ceritellidae, which totally lack folds) similar fold patterns have developed independently. These patterns represent stable configurations and are considered to reflect anatomical features of the living nerineid. It is not clear if these stable fold patterns evolved once, or several times in each family, although the former is considered to be more likely. Further research is required to elucidate evolutionary relationships within the families; if particular fold patterns did evolve only once in a family, then postulated relationships could be based on fold patterns.

At present, systematic relationships between genera are mostly obscure and few workers have attempted to link genera. Pchelintsev (1968) is an exception to this, but unfortunately many of his "family", here considered as subfamily, groupings are based on inconsistent and conflicting criteria and are therefore rejected. An extremely cautious approach to generic and subfamily level taxonomy is recommended. Only species which are very similar morphologically, and have virtually identical fold patterns (with only slight variation in size and positioning) should be placed in the same genus. Genera must be regarded as independent and of uncertain subfamily placement until a clear association of morphologically close genera can be perceived, as, for example, Lysenko and Aliyev (1987) have found, enabling them to erect the Umboneinae (here considered to represent a valid subfamily). In this respect, it is gratifying to note that the wide dichotomy which had developed between Eastern European and Western perceptions of nerineacean systematics, which is demonstrated by comparing table 5.1 with table 5.2, is now considerably narrowed. It is immensely encouraging that recent publications such as Djalilov (1975), Wieczorek (1979) and Lysenko and Aliyev (1987) broadly complement Western perceptions of the group.

Some pre-existing genera are clearly defined and well-established, others are subject to severe nomenclatural problems and/or poor definitions which result in inconsistent interpretations. Revision of such genera is slowly progressing, but

is hampered by the lack of specialist workers. Revised diagnoses for one subfamily and four genera are suggested here, and nomenclatural problems associated with various genera are discussed (Chapter 2).

Most pre-existing Cretaceous species are well-established; their stratigraphic ranges, given here for, in most cases, the first time, indicate for some species a potential application in stratigraphic correlation of Cretaceous Tethyan shelf limestones (see Summary Stratigraphic Range Chart in Appendix 3).

Morphological analysis of over 30 well-preserved *Diozoptyx cochleaeformis* specimens has demonstrated that overall shell shape can vary from isometric to quite markedly cytoconoid, and also that whorl concavity can range widely within one species. In this case, external ornament and internal fold pattern did not vary, indicating that such characters are likely to be of greater reliability in terms of species definition than shell growth form and whorl concavity. The degree of intraspecific variation itself appears to vary from species to species.

Four measured parameters (apical angle, sutural angle, h/w ratio and whorl concavity index) are included in the species descriptions given here. These are of use in two ways; firstly, they provide a guide to the variability present within a species; secondly they can be assessed for their "separation potential" ie how well the parameters used enable cogenetic species to be distinguished.

### 7.3 PALAEOBIOLOGY AND DIVERSITY TRENDS

Evidence of epibiont encrustation and functional analysis of some Cretaceous genera indicate that most were probably mobile epifaunal herbivores, although the elongate shape of Nerinellidae species, which rendered them very susceptible to current influence, are thought to have been mainly infaunal.

The part played by the internal folds remains debatable, although either a support function, perhaps for an additional respiratory structure, or a general strengthening and buoyancy stabilising role are considered to be the most likely possibilities.

Nerineids are largely restricted to tropical and sub-tropical Tethyan areas; they typically inhabited shallow, clear water of normal marine salinity where carbonate deposition was occurring with rudists and corals as other important components of the macrofauna. However, some genera (*Nerinella*, *Eunerinea*, *Aphanoptyxis*) had, by the Cretaceous, become tolerant of other environments associated mainly with back-reef lagoons, where terrigenous influx dominated sedimentation, or, more rarely with deeper water prelittoral situations.

The group suffered its most significant extinction episode between the end of the Cenomanian and the beginning of the Coniacian. The few remaining genera were restricted to prelittoral or sandy nearshore environments and were not associated with rudistid build-ups in the latter part of the late Cretaceous. These genera survived to the Maastrichtian Stage in restricted geographical areas such as the Caribbean which appear to have formed "refuges" where locally high abundances developed. A relatively minor extinction event during the Maastrichtian wiped out these relict genera.

#### 7.4 FURTHER RESEARCH

In the course of this research some problems have been resolved, other have been perceived.

If the group is to fulfil its potential role in the study of Tethyan shelf environments, further work is required. Inconsistencies in the interpretation of pre-existing genera need to be resolved so that an unambiguous taxonomy is available to non-specialists. Further systematic study should enable nerineids to

fulfil a useful stratigraphic correlation function within shallow marine sediments of the Mesozoic.

Evolutionary relationships between genera need to be clarified before widespread subfamily level classification is possible. Further work is required to identify primitive characters and also other features which could be used to describe nerineids before a cladistic approach can be applied to the group.

Documentation of the virtually unreported Cretaceous nerineid fauna of the Americas is quite urgently required. Such a study would help to clarify the stratigraphic and geographic ranges of genera and species, and may help to define evolutionary trends and relationships.



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## APPENDIX 1 LOCALITY DETAILS

NO	NAME	STRATIGRAPHIC POSITION	DETAILS AND FAUNA
7	Calissane Chateau	Upper Barremian (Urgonian facies)	Hilltop 1km N of the chateau, 10km S of Aix-en-Provence, S France <i>Eunerinea vogtiana</i> - very abundant <i>E. archimedi</i> - rare <i>Pchelinsevia coquandiana</i> - very abundant <i>Julesia pellati</i> - rare
17	Brouzet	Upper Barremian	Quarry on N side of D6, 12km E of (Urgonian facies) Arlès, S France <i>E. archimedi</i> - rare <i>P. coquandiana</i> - moderately rare <i>J. pellati</i> - rare
18	Beau Regarde	Upper Barremian (Urgonian facies)	Hillside, 1km SSE of Orgon, 17 km N of Salon-de-Provence, S France <i>E. gigantea</i> - moderately rare
20	La Gabelle	Lower Aptian (Bedoulian)	Roadside exposure, 1km NNW of La Gabelle, 8km E of Sault, S France G1 species 1 - very abundant
34	Lagarde d'Apt	Lower Aptian	Roadside section on D34, 4km N of Lagarde d'Apt, 14km SSE of Sault, S France

			<i>Phaneroptyxis africurgonia</i> - very abundant
35	Combovin	Barremian	Roadside exposure, 0.5km N Combovin on Chateaudouble road, 10km E of Valence, S France <i>J. pellati</i> - rare <i>Aphanoptyxis</i> species - abundant
41	Chodos	Upper Aptian/Lower	Hillside, 0.5km NW Chodos, 40km SW of Morella, Maestrazgo Mountains, NE Spain <i>Eunerinea</i> species - abundant <i>Pchelinsevia</i> species 1
45	Silicified Locality	Upper Hauterivian	Coastal section, 8km NW of Cascais, Sintra Area, Portugal <i>E. vogtiana</i> - abundant <i>E. archimedi</i> - rare <i>P. coquandiana</i> - moderately abundant <i>J. pellati</i> - moderately rare
46	N of 45	Upper Hauterivian/ Lower Barremian	Coastal section, 8.5 - 9km NW of Cascais, Sintra Area, Portugal <i>Diptyxis</i> species 2 - moderately abundant
47	Arriba Resturant	Mid/Upper Barremian	Coastal section, below Arriba Resturant ,10km NW Cascais, Sintra Area, Portugal <i>Aphantoptyxis</i> species 1 -

			moderately abundant <i>Diptyxis ?luttickei</i> - rare
48	Crismina Fort	Lower Aptian	Cliff-top exposure, Crismina Fort, 11km (Bedoulian)NW of Cascais, Sintra Area, Portugal <i>P. toucasiaephila</i> - abundant
51	Cabo da Vide	Upper Albian	Coastal section, 2km S of Ericeira, Portugal. <i>E. ?chloris</i> - rare
52	Comillas	Lower Albian	Coastal section, 1km W of Comillas, 40km W of Santander, N Spain <i>E. chloris</i> - very abundant
60	St Juliao	Lower Aptian (Bedoulian)	Coastal section, 5km S of Ericeira, Portugal <i>D. luttickei</i> - abundant <i>Diptyxis species 1</i> - abundant
61	Ericeira Port	Lower Aptian (Bedoulian)	Coastal section, Port area of Ericeira, Portugal <i>Nerinella species 1</i> - rare
67	Aldeia de Juzo	Upper Valanginian	Roadside section, 0.5km N of Aldeia de Juzo, 3km N of Cascais, Portugal <i>E. guinchoensis</i> - abundant
68	Praia da Luz	Aptian	Coastal section, 1km W of Luz, Algarve, Portugal <i>N. algarbiensis</i> - very abundant

69	Praia do Sol	Albian	Coastal section, 0.5 km S of Ericeira, Portugal <i>Multiptyxis dolomieu</i> - abundant
71	Lanzing	?Upper Santonian/ Lower Campanian	Track section, 0.5km E of Lanzing, 20km W of Wiener Neustadt, Austria <i>Plesioptrygmatis (Simploptyxis) ?buchi</i> - moderately abundant
72	Gams die Noth	Upper Coniacian/ Santonian	Roadside section, 2km E of Gams bei Hieflau, 40km NW of Leoben, Austria <i>P. (S.) pailletteana</i> - abundant
73	Russbach	Santonian	Hillside, 3km N of Russbach, 42km SE of Salzburg, Austria <i>P. (S.) buchi</i> - very abundant
74	Gosau (Edlbach)	Santonian	River section, 1 - 3km NE of Gosau, 46km SE of Salzburg <i>Nerinella</i> species - very abundant
77	Zottbach	Coniacian/Santonian	Hillside and river section, 4km N of Pinegg, 40km E of Kitzbühel <i>P. (S.) ?buchi</i> - rare

## APPENDIX 2 DATA USED IN PARAMETER ANALYSIS

h/w ratio clas	gigantea	vogtiana	archimedi	guincho	chloris
0.45 - 0.47	1	1			
0.48 - 0.50		1			1
0.51 - 0.53		1			3
0.54 - 0.56			1	1	2
0.57 - 0.59			2		4
0.60 - 0.62			1		1
0.63 - 0.65				1	2
0.66 - 0.69					2
whorl concav	gigantea	vogtiana	archimedi	guincho	chloris
0.67 - 0.69		2			
0.70 - 0.72		2	1	1	
0.73 - 0.75		2			
0.76 - 0.78			1	1	
0.79 - 0.81			2		
0.82 - 0.84			2	1	1
0.85 - 0.87	1				
apical angle	gigantea	vogtiana	archimedi	guincho	chloris
13 - 14			3	3	
15 - 16		1			2
17 - 18		2			2
19 - 20					
21 - 22					
23 - 24					
25 - 26	1				
sutural angle	gigantea	vogtiana	archimedi	guincho	chloris
100 - 103	1	1			1
104 - 107		1	1		4
108 - 111		2	1	2	7
112 - 115		1	1		3
116 - 119			2		
	gigantea	gigantea	gigantea	gigantea	gigantea
	gigantea	25	102	0.45	0.86
	vogtiana	vogtiana	vogtiana	vogtiana	vogtiana
			100	0.47	0.71
			110	0.50	0.67
			108	0.53	0.67
	archimedi	archimedi	archimedi	archimedi	archimedi
	archimedi		113	0.57	0.70
			116	0.57	0.78
			107	0.55	0.79
			108	0.60	0.81
	guincho	guincho	guincho	guincho	guincho
	guincho	13	108	0.64	0.82
		14	110	0.55	0.72
	chloris	chloris	chloris	chloris	chloris
	chloris		108	0.56	0.83

Appendix 2a Data used in the *Eunerinea* parameter analysis



Pchelinsevia	Apical angle	coquandiana	toucasiaephila
	18 - 19	2	1
	20 - 21	5	
	22 - 23	5	4
	24 - 25	3	
	26 - 27	3	
	27 - 28	1	
	sutural angle	coquandiana	toucasiaephila
	96 - 99	1	1
	100 - 103	1	3
	104 - 107	3	1
	108 - 111	4	0
	112 - 115	2	1
		h/w ratio	Sutural angle
		coquandiana	coquandiana
		0.41	107
		0.33	114
		0.38	112
		0.46	100
		0.33	109
		0.37	103
		0.39	110
		toucasiaephila	toucasiaephila
		0.23	96
		0.28	102
		0.31	108
		0.36	114
	h/w Ratio	coquandiana	toucasiaephila
	0.22 - 0.28		2
	0.29 - 0.35	3	1
	0.36 - 0.42	5	1
	0.43 - 0.49	1	

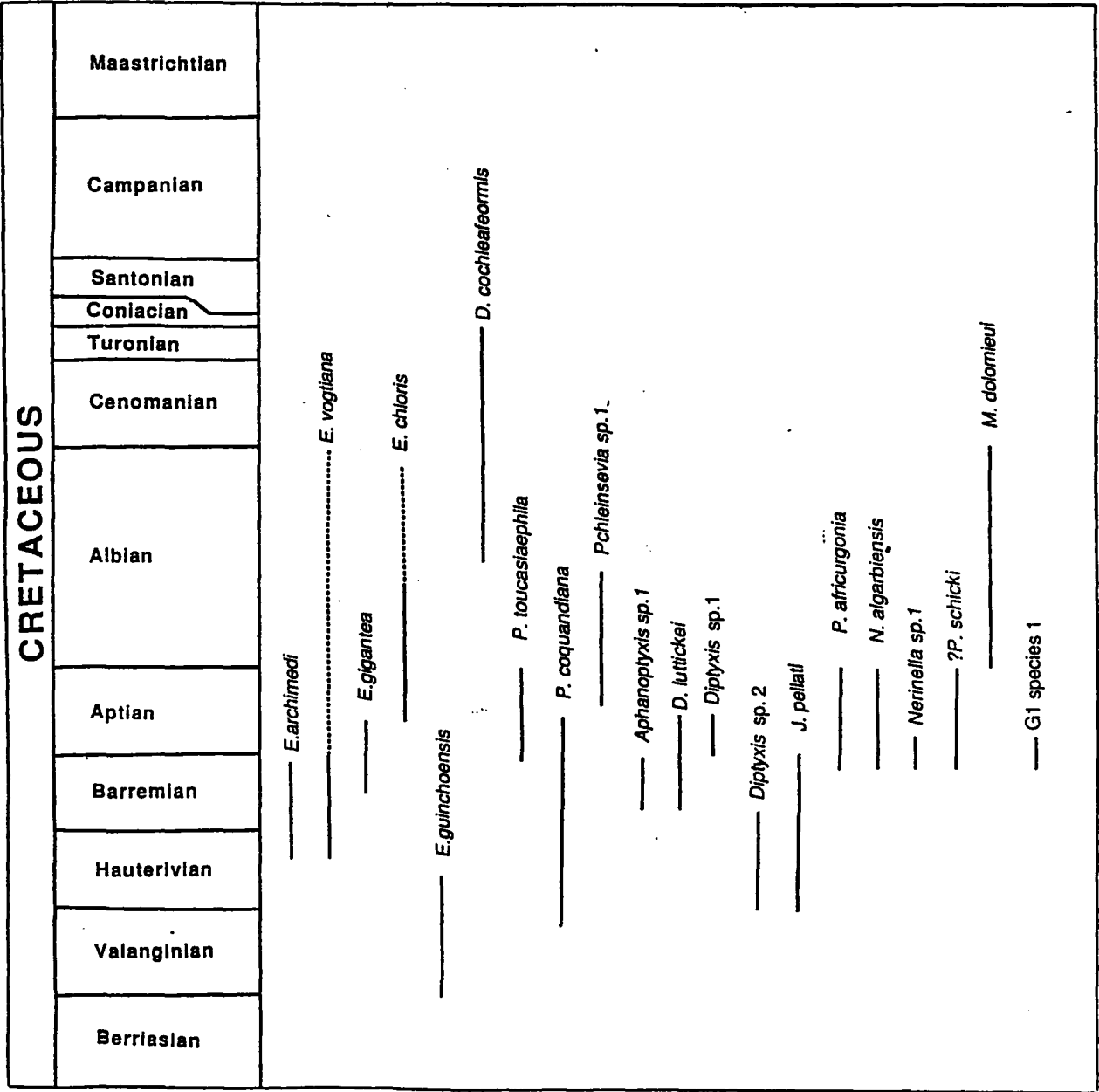
Appendix 2b Data used in the *Pchelinsevia* parameter analysis

# TABLE 2. SUMMARY STRATIGRAPHIC RANGE CHART FOR SPECIES DISCUSSED IN CHAPTER 2

D. cochleaeformis	whorl concav	H/W ratio
	1.15	1.92
	1.3	1.67
	1.2	1.92
	1.22	1.43
	1.19	1.87
	1.3	1.67
	1.25	1.5
	1.2	1.49
	1.32	1.56
	1.25	1.78
	1.28	2.32
	1.32	2
	1.26	1.74
	1.25	2.17
	1.26	1.82
	1.27	1.79
	1.2	1.79
	1.25	1.77
	1.22	1.45
	1.27	1.44
	1.27	1.57
	1.3	1.5
	1.2	1.67
	1.29	1.79
	1.3	2.16
	1.31	1.76
	1.38	1.58
	1.22	1.79
	1.33	1.88
	1.38	1.72
	1.11	2.37

Appendix 2c Data used in *D. cochleaeformis* parameter analysis

# APPENDIX 3 SUMMARY STRATIGRAPHIC RANGE CHART FOR SPECIES DISCUSSED IN CHAPTER 2



Appendix 3 Stratigraphic ranges of Cretaceous species discussed in Chapter 2